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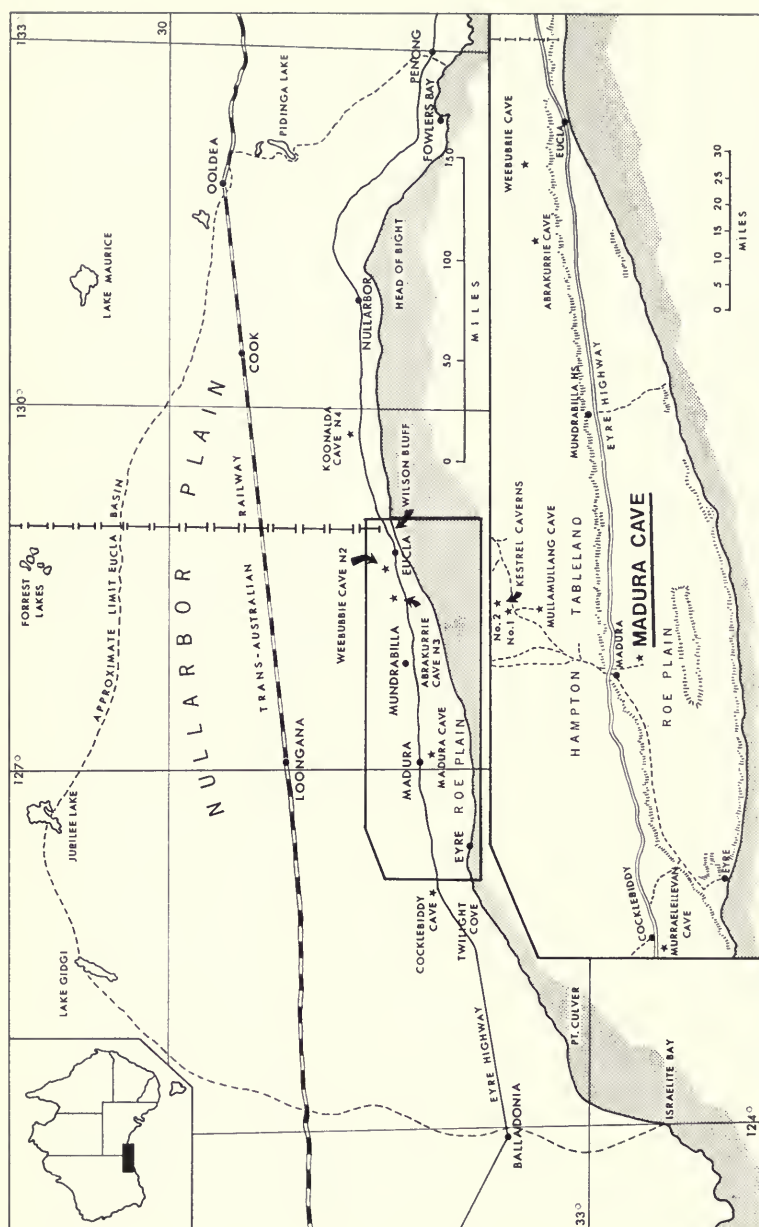
WILLIAM D. TURNBULL

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THE MAMMALIAN FAUNA OF
MADURA CAVE, WESTERN AUSTRALIA
PART IV



FRONTISPIECE. Maps of the Nullarbor Plain area showing Madura Cave on the Roe Plain to seaward of the Hampton Scarp. Also shown are some other nearby caves on the Hampton Tableland, above the scarp.*

FIELDIANA

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THE MAMMALIAN FAUNA OF MADURA CAVE, WESTERN AUSTRALIA PART IV

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ABSTRACT

The peramelids represented in the Madura Cave deposits are *Perameles bougainvillei*, *Isoodon obesulus*, *Chaeropus ecaudatus*, and *Macrotylis lagotis*.

Perameles bougainvillei is found in abundance in all stratigraphic units. Specimens from unit 1 (7420 B.P. and younger) show no qualitative differences from those in units 2 through 4-5 (15,000-22,000 B.P.). Post-Pleistocene reduction in size is indicated by significant differences in three of nine dental measures tested ($P < .05$, one sided "t" test).

Chaeropus ecaudatus and *Macrotylis lagotis* are represented in all units and are known from the Nullarbor Plain in historic times. No morphological changes in these species are seen in the period of time represented by the Madura Cave deposits.

Isoodon obesulus is present in all units except unit 7. Its absence from unit 7 is possibly a sampling accident. The recovered specimens are intermediate in size between specimens of *I. obesulus* from southwestern Australia and Victoria and specimens of *I. auratus*, but they are closer to the former. No morphological differences are seen between the specimens from units 4-5 and unit 1. This taxon is not known to have been present on the Nullarbor Plain in historic time. Its presence in early Holocene deposits suggests a change to drier climatic conditions in this region during this time.

INTRODUCTION

This section of the Madura Cave work continues the systematic section begun in Part I (1973) and continued in Parts II (1975) and III (1978), in which 14 taxa of the Dasyuroidea and one of Thylacoleonidae were covered. Here we consider the Order Peramelina, which is represented in the Madura Cave deposits by at least four taxa: the very abundant *Peramelus bougainvillei* and smaller numbers of *Isoodon obesulus*, *Chaeropus ecaudatus*, and *Macrotylis lagotis*.

Madura Cave is located on the Roe Plain 6 miles (9.6 km) south of the settlement of Madura, 110 miles (177 km) west of Eucla (see frontispiece). The cave system consists of a shallow oval doline whose long axis is oriented NW-SE, with two tunnels extending outward from its margins. One tunnel extends southwestward from the doline's southern end, the other northwestward from its northern end. No excavations were carried out in the southern tunnel.

The northern tunnel, which is much larger than the southern tunnel, has a floor 8-10 ft lower than the surface of the doline and a gentle gradient toward the back of the cave.

Five trenches were dug in the northern tunnel, two by Lundelius in 1955 and

three by us in 1964. The stratigraphic sequence in trenches 3 and 4, which produced the most faunal material, consists of the following: a top unit (unit 1 of both trenches) of loose, gray brown silt with many limestone fragments, abundant small bones, and organic material. This unit is separated from the underlying material by an irregular surface. A C-14 date (TX 1146) of $7,470 \pm 120$ B.P. was obtained from the top foot of this unit in trench 4.

A sequence of red, clayey silts, sands, and limestone powder underlies unit 1. The following C-14 dates were obtained:

Trench 3

Unit 2, upper 1 ft, $15,600 \pm 250$ years B.P. (TX 1145)

Unit 2, lower 1 ft, $22,400 \pm 580$ years B.P. (TX 1142)

Trench 4

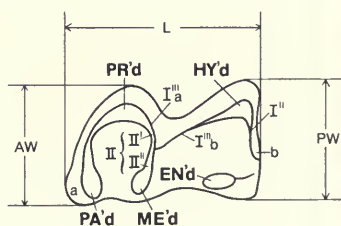
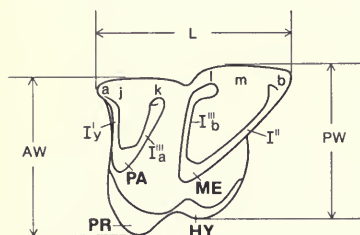
Unit 2, upper 6 inches, $18,990 \pm 220$ years B.P. (TX 1140)

Unit 2, 6–12 inches, $20,000 \pm 430$ years B.P. (TX 1141)

Units 4–5, $22,220 \pm 570$ years B.P. (TX 1144)

Unit 7, lower 1 ft, exposed: $37,880 \pm 3,520$ years B.P. (TX 1143)

Measurements and abbreviations used are either those in standard use or they have been outlined in one of the prior sections. The dental terminology has recently been summarized by HersHKovitz (1971), and the reader is referred to that work as containing the most complete compilation of terms and abbreviations available. Those we use are all listed there. The diagrams below indicate the manner used in taking the dental measures: L (=length), AW (=anterior width), PW (=posterior width). They also show some of the HersHKovitz symbols for certain of the styler cusps and segments of the eocrista(id) that are convenient designations. Major cusp abbreviations follow the Cope-Osborne standard.



SYSTEMATICS (section continued)

Class Mammalia (continued)

Subclass Theria (continued)

Infraclass Eutheria (continued)

Cohort Marsupiiata (*sensu* Turnbull, 1971: = Metatheria) (continued)

Order Peramelina (Gray, 1825; revised Ride, 1964)

Family Peramelidae (Waterhouse, 1838, 1841)

Perameles Geoffroy, 1803, 1804

Perameles bougainvillei Quoy and Gaimard, 1824

MATERIAL

Trench 1, top 1 ft

Lundelius (1963) listed *P. bougainvillei* as occurring in this level, but he gave no catalogue numbers, and we've not been able to locate specimens so assigned. Apparently they have been misplaced.

Trench 1, top 30 inches

PM 26183, right ramus with M₃ and alveoli of all other cheek teeth

PM 26184, left ramus with M₃ and alveoli of P₄-M₂ and M₄

PM 26185, edentulous left maxillary fragment with alveoli of premolars and M¹⁻²

Trench 2, 2½ ft below surface

PM 25223, edentulous left ramus fragment with alveoli of P₄-M₄

PM 25225, left ramus fragment with M₂₋₃ and alveoli of M₁ and M₄

PM 25226, right ramus fragment with M₄ and alveoli of M₂₋₃

Trench 3, Unit 2, Level 1

TMM 41106-68, left mandible with P₄ and alveoli of rest of cheek teeth

TMM 41106-69, left ramus fragment with P₄ and alveoli of P₁₋₃ and M₁₋₃

TMM 41106-70, right mandible with M₃₋₄ and alveoli of I₃ and rest of teeth to M₃

TMM 41106-71, right ramus fragment with M₄ and alveoli of M₁₋₃

TMM 41106-72, right ramus fragment with C, P₃₋₄ and alveoli of I₃, P₁, M₂₋₃

TMM 41106-73, right ramus fragment with broken M₄ and alveoli of M₂₋₃

TMM 41106-74, right ramus with M₃₋₄ and alveoli of premolars and M₁₋₂

TMM 41106-75, right ramus with M₄ and alveoli of C-M₃

TMM 41106-76, left ramus fragment with M₁₋₃ and alveoli of I₃ through P₄

TMM 41106-77, left mandible with C, P₁ or 2, P₄, M₁, M₃₋₄ and alveoli of incisors and intervening teeth (fig. 6A, B)

TMM 41106-78, left mandible with P₄ and M₄ and alveoli of C and rest of cheek teeth

TMM 41106-79, right mandible with M₃₋₄ and alveoli of C-M₂

TMM 41106-80, right ramus fragment with M₃ and alveoli of I₂-M₂

TMM 41106-81, left ramus fragment with P₄ and alveoli of C-P₃, M₁₋₂

TMM 41106-82, left ramus fragment with M₄

TMM 41106-363, right maxillary with P³⁻⁴, M¹, alveoli of rest of cheek teeth (fig. 4A, B)

TMM 41106-2753, left mandible with C-M₄, (P₃ broken), alveoli of I₁₋₃ (fig. 7A, B, C)

PM 13339, edentulous right maxillary with alveoli for P², M⁴

PM 13340, right maxillary with M²⁻³, alveoli for P³-M¹ and M⁴ (fig. 4C, D)

PM 13341, left maxillary with P³, alveoli for P², P⁴, M¹

PM 13342, right maxillary with M², alveoli for M³⁻⁴

PM 25584, right ramus fragment with C

PM 25585, left ramus fragment with parts of C and P₁ or 2

PM 26990, left ramus fragment with M₄ and alveoli of M₃

PM 26991, right ramus fragment with P₄ and alveoli of C-P₃

PM 26992, right ramus fragment with broken P₄ and alveoli of P₁₋₃, M₁₋₃

Trench 3, Unit 2, Level 1 (continued)

- PM 26993, left ramus fragment with M₃ and alveoli of M₂ and M₄
- PM 26994, left ramus with M₄ in crypt, alveoli of P₃-M₃
- PM 26995, right ramus fragment with P₄, alveoli of C-P₃ and M₁₋₃
- PM 26996, left ramus fragment with P₃₋₄, alveoli of M₁
- PM 26997-8, two right M₁s
- PM 26999-7002, four left M₁s
- PM 27003-23, 21 right M₂s or M₃s
- PM 27024-40, 17 left M₂s or M₃s
- PM 27041-3, three left M₄s
- PM 27044-5, two right M₄s
- PM 27046-9, four right M₁s
- PM 27050-4, five left M₁s
- PM 27055-75, 21 left M₂s or M₃s
- PM 27076-90, 15 right M₂s or M₃s
- PM 27091-2, two left M₄s
- uncatalogued, ca. 100 edentulous ramus and maxillary fragments
- uncatalogued, two specimens with label lost, probably this level
- uncatalogued, one vial with hundreds of uncatalogued premolars

Trench 3, Unit 2, Level 2

- TMM 41106-43, ?*Perameles* cranium
- TMM 41106-322, left M¹
- TMM 41106-2755, right M⁴
- TMM 41106-2756-9, four right M¹s
- WAM 74.9.52-.53, two left M²s or M³s
- WAM 74.9.54, right M₄
- WAM 74.9.55, left M₁
- PM 27093-112, 20 left M²s or M³s
- PM 27113-5, three right M₄s
- PM 27116-7, two left M₁s
- PM 27118-20, three right M₁s
- PM 27121-9, nine right M₂s or M₃s
- PM 27130-2, three premolars
- PM 27133-40, eight right M²s or M³s
- PM 27141-52, 12 left M₂s or M₃s
- PM 27219, left M₄

Trench 3, Unit 2, Level 4

- TMM 41106-399, right ramus fragment with M₄, coronoid, and condyle
- TMM 41106-400, right ramus fragment with M₃₋₄, coronoid, and condyle
- TMM 41106-402, right ramus fragment with M₃₋₄, alveoli of M₁₋₂, coronoid, and condyle
- TMM 41106-405, right ramus fragment with P₄, alveoli of C-P₃
- TMM 41106-408, right ramus fragment with P₂ and P₃, alveoli of P₄-M₂
- TMM 41106-414, right maxillary fragment with M¹, alveoli of P³⁻⁴
- PM 27162, left maxillary fragment with M² or ³
- PM 27163, left maxillary fragment with M¹, alveoli of M²
- PM 27164-5, two edentulous left maxillary fragments
- PM 27166-71, five edentulous right maxillary fragments

Trench 3, Unit 3

- TMM 41106-38, left ramus with alveoli of C-M₃
- TMM 41106-39, left ramus with alveoli of P₂-M₄
- TMM 41106-40, left ramus with alveoli of M₁-M₄
- TMM 41106-41, right ramus with P₂, alveoli of P₃-M₃
- TMM 41106-42, right ramus with alveoli of M₃, M₄
- TMM 41106-2764, left ramus with M₄, alveoli of M₂₋₃
- TMM 41106-2765, right ramus with M₄, alveoli of M₃
- TMM 41106-2766, left ramus with M₂ or M₃, alveoli of P₄-M₁ or M₁₋₂
- TMM 41106-2754, left ramus alveoli of M₁-M₄
- TMM 41106-2760, edentulous left maxillary
- TMM 41106-2761, left maxillary fragment with M³ and alveoli of M² and M⁴
- TMM 41106-2762, right M¹
- uncatalogued, two edentulous ramus fragments

Trench 4, Unit 1, Level 1

- TMM 41106-475, right M¹
- TMM 41106-507, 10 edentulous mandibular fragments
- TMM 41106-508, left maxillary fragment with P³, alveoli of P², P⁴, and M¹
- TMM 41106-509, left P₃
- TMM 41106-512, right maxillary fragment with M¹⁻⁴ (fig. 4E, F)
- TMM 41106-513, right maxillary fragment with M³⁻⁴
- TMM 41106-514, left ramus fragment with P₄, alveoli of P₃, and M₁
- TMM 41106-515, premolar
- TMM 41106-518, edentulous left maxillary fragment with palatal bar and foramina, alveoli of P¹, P³, and P⁴, and M¹. P⁴ is within crypt.
- TMM 41106-549, left M³
- TMM 41106-550, left M¹
- TMM 41106-678, left M₂
- TMM 41106-5089, edentulous maxillary fragment
- TMM 41106-5090, four edentulous maxillary fragments
- TMM 41106-5091, two right M²s
- TMM 41106-5092, right M³
- TMM 41106-5093, three edentulous right ramus fragments
- TMM 41106-5094, two edentulous left ramus fragments
- TMM 41106-5095, three left M₂s
- TMM 41106-5096, left M¹
- TMM 41106-5097, right M¹
- PM 27153-4, two left M²s
- PM 27155, left M³
- PM 27156, left M²
- PM 27157-8, right and left M¹s
- PM 27159-61, three right M²s
- PM 27172-4, three left M₂s
- PM 27175, left M₃
- PM 27176, right M₄ talonid
- PM 27177-8, two right M₁s
- PM 27179-80, two left M_x fragments
- PM 27181-3, two left M₁s and one right M₁

Trench 4, Unit 1, Level 1 (continued)

- PM 27184, broken right M₂ or 3
- PM 27185, right M₂
- PM 27186, broken right M₂ or 3
- PM 27187-8, two right M₁s
- PM 27189, right M¹
- PM 27190, right M^{1,2.} or 3, probably M²
- PM 27191-2, left and right M¹s
- PM 27193, premolar
- PM 27194-5, edentulous left and right maxillary fragments
- PM 27196, edentulous ramus fragment
- PM 27197, left M₃
- PM 27198-9, right and left M₂s
- PM 27200, premolar
- PM 27201, left ramus fragment with M₄ in crypt, alveoli of M₃
- PM 27202, edentulous right mandible
- PM 27203-6, four edentulous left ramus fragments
- PM 27207, one left, one right edentulous maxillary fragment
- PM 27208, right I³
- PM 27209, left M₃
- PM 27210, left M₁
- PM 27211, left M₃
- PM 27212-14, three left M₂s
- PM 27215, left M₃
- PM 27216, broken left M₂ or 3
- PM 27217, left M₃
- PM 27220-21, two right M₁s
- PM 27222, right M₂
- PM 27223, right M₃
- PM 27224, left M₂
- PM 27225, left M₃
- PM 27226-7, two left M₂s
- PM 27228, left M₃
- PM 27229-30, two right M₃s
- PM 27231-6, six right M₂s

Trench 4, Unit 2, Level 1

- PM 27237, right mandible with M₄, alveoli of other teeth
- PM 27238, right mandible with P₄, M₃₋₄, alveoli of rest of teeth (fig. 5C, D)
- PM 27239, left ramus fragment with M₃, alveoli of premolars, and other molars
- PM 27240, left mandible edentulous except for parts of C and P₄
- PM 27241, left ascending ramus fragment with coronoid, condyle, and angular process
- PM 27242, right mandible with P₂, P₄, M₃₋₄, alveoli of other teeth (fig. 6C, D)
- PM 27243, left ramus fragment with M₄ in crypt, alveoli of P₄-M₃
- PM 27244, left maxillary fragment with M² or M³
- PM 27245, edentulous left ramus with alveoli of P₃-M₄
- PM 27246, edentulous right ramus fragment with alveoli of M₃₋₄

Trench 4, Unit 2, Level 1 (continued)

- PM 27247, edentulous right ramus fragment with alveoli of P₃-M₃
- PM 27248, edentulous right ramus fragment with alveoli of M₄
- PM 27249, edentulous left ramus fragment with alveoli of M₂₋₃?
- PM 27250, edentulous right ramus fragment with alveoli of C-P₄
- PM 27251, edentulous left ramus fragment with alveoli of C-P₂
- PM 27252, edentulous right ramus fragment with alveoli of P₃-M₁
- PM 27253, edentulous left ramus fragment with alveoli of P₁₋₄
- PM 27254, edentulous ramus fragment with alveoli of premolars
- PM 27255, left ramus fragment with P₂, alveoli of P₃₋₄
- PM 27256, edentulous left maxillary fragment with alveoli of P³-M³
- PM 27257, left ramus fragment with P₁, alveoli of I₃, C, P₃
- PM 27258, edentulous left mandible with coronoid, condyle, and part of angular process
- PM 27259, edentulous right maxillary fragment with alveoli of P³, dP⁴, M¹
- PM 27260, edentulous left maxillary fragment with alveoli of cheek teeth
- PM 27261-8, eight right M¹s
- PM 27269-75, seven left M²s or M³s
- PM 27276, edentulous left ramus fragment with alveoli of I₃-M₂
- PM 27277, left ramus fragment with P₂ and P₃, alveoli of P₄-M₂
- PM 27278, edentulous left ramus fragment with angle, coronoid, and condyle
- PM 27279, edentulous right ramus fragment with alveoli of M₁₋₄
- PM 27280, left ramus fragment with P₄, alveoli of I₃-P₃
- PM 27281, edentulous left ramus fragment with alveoli of M₃₋₄
- PM 27282, edentulous right ramus fragment with alveoli of C-M₂
- PM 27283-5, three edentulous right ramus fragments with alveoli of M₃₋₄
- PM 27286, edentulous right ramus fragment with alveoli of P₂-M₃
- PM 27287, edentulous left ramus fragment with alveoli of C-P₃
- PM 27288, edentulous right ramus fragment with alveoli of M₃₋₄, portion of angle
- PM 27289, edentulous left ramus fragment with alveoli of P₁₋₃
- PM 27290, edentulous right ramus fragment with alveoli of premolars
- PM 27291, edentulous left ramus fragment with alveoli of M₄
- PM 27292, edentulous left ramus fragment with alveoli of P₄-M₂
- PM 27293, edentulous left ramus fragment with alveoli of premolars
- PM 27294, right maxillary fragment with M⁴, alveoli of P⁴-M³
- PM 27295, left M₁
- PM 27296-7, two premolars
- PM 27298, edentulous right maxillary fragment with alveoli of P⁴, M¹
- PM 27299-300, two right M²s or M³s
- PM 27301-7, seven left M¹s
- PM 27308-12, five left M₁s
- PM 27313-9, seven right M₁s
- PM 27320-37, 18 left M₂s or M₃s
- PM 27338-63, 26 M²s or M³s
- PM 27364, left M⁴
- PM 27365-8, four left M⁴s
- PM 27369-99, 31 right M₂s or M₃s

Trench 4, Unit 2, Level 2

- TMM 41106-713, right M² or ³
TMM 41106-2767, premolar
TMM 41106-2768, left M² or ³
TMM 41106-2769, partial left upper molar
TMM 41106-2770, left P⁴
TMM 41106-2771, left mandible with M₃₋₄, alveoli of rest of teeth (fig. 5A, B)
TMM 41106-2772, edentulous left ramus with coronoid, condyle, angle, and alveoli of P₄-M₄
TMM 41106-2773, left ramus fragment with M₄ in crypt, alveoli of M₃
TMM 41106-2774, edentulous left ramus fragment with alveoli of M₁₋₄
TMM 41106-2775, edentulous left mandible with alveoli of all teeth
TMM 41106-2776, left maxillary with P³, alveoli of rest of cheek teeth
TMM 41106-2777, left maxillary fragment with P³
TMM 41106-2778, two right maxillary fragments, one with P¹, the other with P⁴, probably same individual
TMM 41106-2779, left ramus fragment with M₃, alveoli of M₁₋₂
TMM 41106-2780, left ramus fragment with P₃, alveoli of I₃-P₁
TMM 41106-2781, right ramus fragment with M₄, alveoli of P₃-M₃
TMM 41106-2782, edentulous right ramus fragment with alveoli of all cheek teeth
TMM 41106-2783, edentulous right ramus fragment with coronoid, condyle, angle, and alveoli of M₄
TMM 41106-2784, edentulous right ramus fragment with broken P₁, P₄, M₁, alveoli of C-P₃
TMM 41106-2785, right ramus fragment with M₄, alveoli of P₃-M₃
TMM 41106-2786, right ramus fragment with P₃, alveoli of P₄-M₂
TMM 41106-2787, edentulous right ramus fragment with alveoli of M₃₋₄, coronoid, and condyle
TMM 41106-2788-95, eight left M₁s
TMM 41106-2796, right M₁ fragment
TMM 41106-2797-804, eight right M₁s
TMM 41106-2805, right M¹ fragment
TMM 41106-2806-10, five left M₄s
TMM 41106-2811-3, three right M₄s
TMM 41106-2814-6, three left M₄s
TMM 41106-2817-9, three left M₁s
TMM 41106-2820-7, eight left M²s or M³s
TMM 41106-5098, 20 edentulous ramus fragments
WAM 75.1.1-.5, five left M₁s
WAM 75.1.6-.11, six right M₁s
WAM 75.1.12-.16, five left M²s or M³s
PM 27400-425, 26 right M₂s or M₃s
PM 27426-7, two right M₂s or M₃s
PM 27428-452, 25 right M²s or M³s
PM 27453-460, eight right M₄s
PM 27461, right M² or M³
PM 27462-9, eight left M²s or M³s

Trench 4, Unit 2, Level 2 (continued)

- PM 27470-3, four left M¹s
- Pm 27474-8, five right M¹s
- PM 27479-517, 39 left M²s or M³s
- PM 27518-96, 79 premolars
- uncatalogued, 46 incisors or canines

Trench 4, Unit 2, Level 3

- PM 27597-9, three left M¹s
- PM 27600-1, two left M²s or M³s
- PM 27602-4, three right M²s or M³s
- PM 27605-8, four right M¹s
- PM 27609-10, two left M²s or M³s
- PM 27611, left lower molar fragment
- PM 27612-3, two premolars
- PM 27614-21, eight right M²s or M³s
- uncatalogued, six edentulous maxillary fragments
- uncatalogued, 21 edentulous ramus fragments

Trench 4, Units 4-5

- TMM 41106-718, right M² or ³
- TMM 41106-728, trigonid of left M_x
- TMM 41106-3001-85, 85 right M¹s
- TMM 41106-3086-171, 86 left M¹s
- TMM 41106-3172-221, 50 left M⁴s
- TMM 41106-3222-72, 51 right M⁴s
- TMM 41106-3273-312, 40 left M²s or M³s
- TMM 41106-3313-41, 29 left M¹s
- TMM 41106-3342-58, 17 left M⁴s
- TMM 41106-3359-90, 31 right M⁴s
- TMM 41106-3391-444, 54 right M¹s
- TMM 41106-3445-65, 21 right M²s
- TMM 41106-3466-99, 34 right M³s
- WAM 75.1.17, left ramus with M¹
- WAM 75.1.18, right ramus with M₃₋₄
- WAM 75.1.19, left mandible, edentulous except for C
- WAM 75.1.20, edentulous left mandible
- WAM 75.1.21-.26, six left M¹s
- WAM 75.1.27-.32, six left M⁴s
- WAM 75.1.33-.38, six right M⁴s
- WAM 75.1.39-.50, 12 left M²s or M³s (probably M²)
- WAM 75.1.51-.62, 12 left M²s or M³s (probably M³)
- WAM 75.1.63-.68, six left M¹s
- WAM 75.1.69-.72, four left M⁴s
- WAM 75.1.73-.77, five right M⁴s
- WAM 75.1.78-.82, five right M¹s
- WAM 75.1.83-.92, 10 right M³s (measured)
- WAM 75.1.93-.99, seven right M²s
- WAM 75.1.100-.103, four right M²s or M³s
- WAM 75.1.104-.110, six right M²s
- WAM 75.1.111, right M² or M³

Trench 4, Units 4-5 (continued)

- WAM 75.1.112-.114, three right M¹s
WAM 75.1.115-.117, two right P⁴s and a left P⁴
PM 13401-20A, 40 right M₂s or M₃s
PM 26318-9, two left M₁s
PM 26330, left M²
PM 27622, right ramus with P₃
PM 27623, left ramus with P_x
PM 27624, premolar
PM 27625, trigonid, left M_x
PM 27626, edentulous right ramus
PM 27627, edentulous left ramus fragment, alveoli of M₃₋₄
PM 27628-9, two edentulous right ramus fragments, alveoli of M₃₋₄
PM 27630, edentulous right ramus fragment, alveoli of P₂-M₁
PM 27631, edentulous left ramus fragment, alveoli of P₂-M₁
PM 27632, edentulous right ramus fragment, alveoli of P₂-M₁
PM 27633, edentulous left ramus, alveoli of cheek teeth
PM 27634, edentulous right maxillary, alveoli of M¹⁻⁴
PM 27635, left M₄
PM 27636, right M₄ in ramus fragment
PM 27637, left M₄ in crypt, ramus angle, alveoli of M₂₋₃
PM 27638, left P₃ in ramus fragment
PM 27639, edentulous right ramus
PM 27640, left edentulous ramus, alveoli of M₁₋₄
PM 27641 (A-G), seven edentulous right ramus fragments
PM 27642 (A-H), -43 (A-F), and -44 (A-F), 20 edentulous right ramus fragments
PM 27645 (A-E) and -46 (A-E), 10 edentulous left ramus fragments
PM 27647 (A-E) and -48 (A-F), 11 edentulous left ramus fragments
PM 27649-675, 27 right M₂s or M₃s
PM 27676-89, 14 left M₂s or M₃s
PM 27690, right M₂ or ₃
PM 27691-739 and PM 27741-52, 61 left M₂s or M₃s
PM 27753-7, five right M₂s or M₃s
PM 27758, left M₂ or M₃
PM 27759-85, 27 right M₂s or M₃s
PM 27786-801, 16 right M₄s
PM 27802-22, 21 right M₁s
PM 27825-30, six left M₄s
PM 27831-46, 16 left M¹s
PM 27847-66, 20 left M₁s
PM 27867, right M⁴
PM 27868-92, 35 right M¹s
PM 27893-902, 10 premolars
PM 27903-8, six right M²s or M³s
PM 27909-15, seven left M₄s
PM 27916-28, 13 right M₄s
PM 27929-30, two left M₄s
PM 27946-68, 23 left M₂s (measured)

Trench 4, Units 4-5 (continued)

- PM 27969-80, 12 left M₂s or M₃s (probably M₂s)
- PM 33501-63, 63 left M₂s or M₃s (probably M₂s)
- PM 33564-610, 47 left M₂s or M₃s (probably M₃s) (33564-89 measured)
- PM 33611-24, 14 left P⁴s
- PM 33625-8, four left M₁s
- PM 33629 (A-Z), PM 33630 (A-AA), and PM 33631 (A-M), 66 right M²s or M³s
- PM 33632-58, 27 left M¹s
- PM 33659 (A-C), three broken left M¹s
- PM 33663-92, 30 left M²s or M³s
- PM 33693-732, 40 left M²s
- PM 33733-6, four right P⁴s
- PM 33737-69, 33 left M²s
- PM 33770 (A-EE), 31 broken left M²s or M³s
- PM 33771-2, two left M¹s
- PM 33773-872, 100 left M³s
- PM 33873 (A-Y), PM 33874 (A-XX), and PM 33875 (A-N), 89 indet. pre-molars (no P⁴s)
- PM 33876 (A-L), PM 33877 (A-N), and PM 33878 (A-VV), 74 indet. pre-molars
- PM 33879 (A-FFFFF), 110 indet. premolars
- uncatalogued, ~400 isolated premolars
- PM 33880 (A-AA), -81 (A-Z), and -82 (A-M), 56 broken right M₂s or M₃s
- PM 33883-7, five right M₁s
- PM 33888-91, four right M₁s or M₂s, (probably M₁s)
- PM 33892-4054, 163 right M₂s or M₃s
- PM 34055-6, two left M₄s
- PM 34057-64, eight right P⁴s
- PM 34065-84, 20 right M²s or M³s
- PM 34085-107, 23 right M²s (measured)
- PM 34108 (A-Z), 26 broken left M_xs
- PM 34109 (A-U) and PM 34110 (A-U), 42 broken M_xs
- PM 34111-26 (A-P), 16 right M³s (measured)
- PM 34127-37, 11 right M¹s
- PM 34138-59, 22 right M²s or M³s
- PM 34160 (A-ZZZ), 78 edentulous left ramus fragments
- PM 34161 (A-DDDD), 82 edentulous right ramus fragments
- PM 34162, five broken right M_xs
- PM 34163, broken M^x
- PM 34165, right mandible with M₄ in crypt
- PM 34166, right mandible with M₄
- PM 34167, right mandible with P₃, M₂₋₃
- PM 34168 (A-B), two broken left M_xs
- PM 34169, left maxillary with M⁴, alveoli of P⁴-M³
- PM 34170, premolar
- PM 34171 (A-B), fragments of two premolars
- PM 34173 (A-H), eight upper incisors

Trench 4, Units 4-5 (continued)

PM 34174 (A-C), three I₁s or I₂sPM 34175 (A-F), six left I₃sPM 34176 (A-M), 13 right I₃s

Trench 4, Unit 7, Level 1

TMM 41106-707, right M² or ³WAM 75.1.119, right M₄WAM 75.1.120-1, two left M₂s or M₃sWAM 75.1.122, right M₂ or M₃PM 34177, right M₄PM 34179, left M₁PM 34180, edentulous right maxillary fragment with alveoli of P³PM 34181, edentulous right ramus fragment with alveoli of M₄

PM 34182 (A-B), two edentulous left ramus fragments

PM 34183-94, 12 left M₂s or M₃sPM 34195, right M₁PM 34196-9, four left M¹sPM 34200-3, four right M³sPM 34204-8, five right M²sPM 34209, right M² or M³PM 34210, right M₄PM 34211-2, two left M²sPM 34213-4, two right M¹sPM 34215-8, four left M³sPM 34219-31, 13 right M₂s or M₃s

Trench 4, Unit 7, Level ?

PM 34232, right ramus fragment with M₄ in cryptPM 34233, left P⁴PM 34234, right ramus fragment with M₃₋₄

PM 34235, edentulous right ramus

PM 34236 (A-B), C-G, two left and five right edentulous ramus fragments

Trench 4, Unit 7, Level 2

TMM 41106-730, broken left M₄WAM 75.1.123, left M₁PM 34237-9, three right M₁sPM 34240-8, nine left M₁sPM 34249, left ramus fragment with P₄ in crypt

PM 34250, (A-B, C-H), two right and six left edentulous ramus fragments

PM 34253-4, two left M₄sPM 34256-9, four left M¹sPM 34260-4, five right M¹sPM 34265-7, three right M³sPM 34268-9, two right M²sPM 34270-5, six left M²sPM 34276-8, three left M³sPM 34279-80, two left M²s or M³sPM 34281, left M⁴PM 34282-5, four right M₄s

Trench 4, Unit 7, Level 2 (continued)

- PM 34286-94, nine left M₂s or M₃s
- PM 34295, left M₁
- PM 34296 (A-C), three broken left M₂s or M₃s
- PM 34297-314, 18 right M₂s or M₃s
- PM 34315, broken right M₂ or M₃
- PM 34316, right M₁

Trench 5, Unit 4

- PM 34317, right P⁴
- PM 34318, right M¹
- PM 34319, right M²
- PM 34320, right M³
- PM 34321-2, two left M¹s
- PM 34323-5, three left M²s
- PM 34326, left M³
- PM 34327 (A-B), two edentulous right ramus fragments
- PM 34328 (A-E), five edentulous left ramus fragments
- PM 34329 (A-D), four edentulous left maxillary fragments
- PM 34330 (A-D), four edentulous right maxillary fragments
- PM 34331, left M₄

Trench 5, Unit 5

- TMM 41106-692-3, edentulous right and left rami, respectively
- PM 26332, broken right M¹ or M²
- PM 34332 (A-B), right and left maxillary fragments, each with P³
- PM 34333, edentulous left maxillary fragment
- PM 34334 (A-C), three edentulous left ramus fragments
- PM 34335, edentulous right ramus fragment
- PM 34336, right cranial fragment
- PM 34337-9, three left M₁s
- PM 34340-1, two right M₁s
- PM 34342-8, seven right M₂s or M₃s
- PM 34349-54, six right M₃s
- PM 34355, left M₄
- PM 34356, broken left M^{1, 2, or 3}
- PM 34357, broken right M₂ or M₃
- PM 34358-64, seven left M₂s or M₃s
- PM 34365, left M₃ or M₂
- PM 34366, left P₁?
- PM 34367-75, nine left P₃s
- PM 34376-9, four left P₄s or P₃s
- PM 34380, left P⁴
- PM 34381-3, three right P₄s or P₃s
- PM 34384-7, four left M₂s or M₃s
- PM 34388-9, two left M¹s
- PM 34390-95, six left M³s or M²s
- PM 34396-7, three left M³s
- PM 34398, left M⁴
- PM 34399-402, four right M¹s
- PM 34403-6, four right M²s

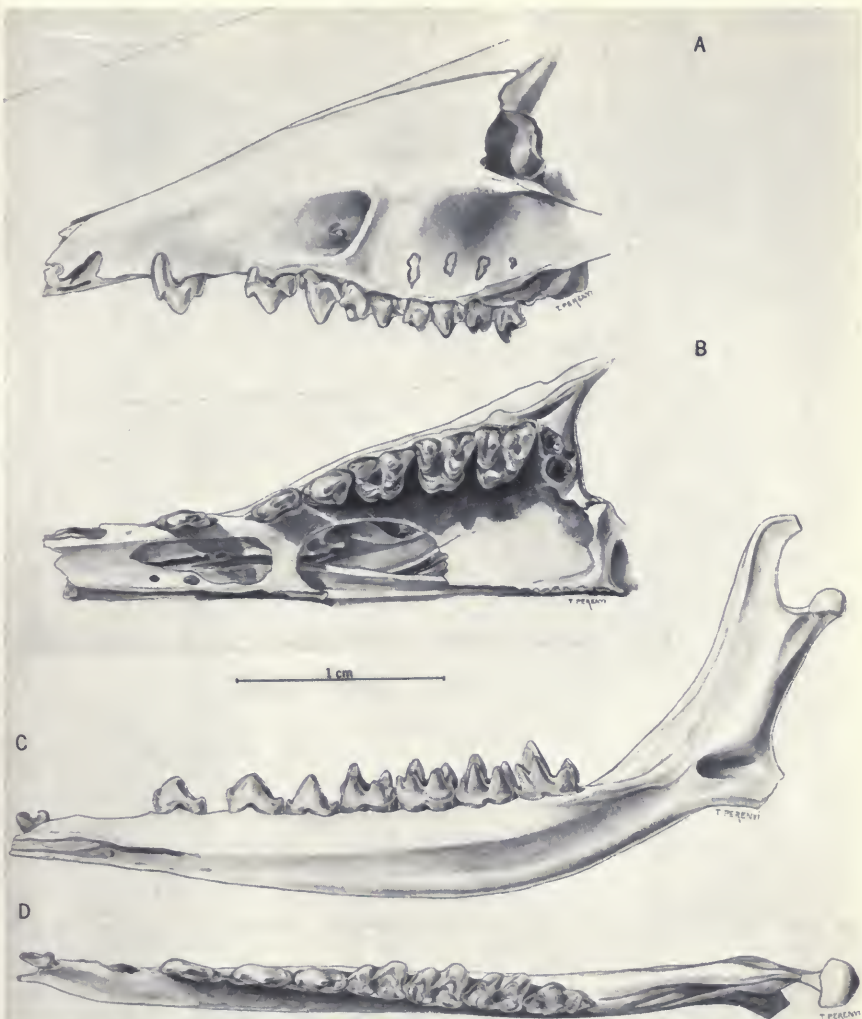


FIG. 1. *Perameles bougainvillei*, TMM-40235-2, a subfossil specimen from the surface of Murraelellavan Cave, Nullarbor Plain, Western Australia. A & B, Left lateral and ventral views of the facial portion of the skull and its dentition. C & D, Lingual and crown views of the right ramus and its dentition.

posteriorly. Cingular cusps are present on the anterior and posterior ends of the tooth. A prominent lingual cingular shelf with a cuspsule is present. It varies considerably in size and position. In specimen TMM 41106-363, it is located lingual to the main cusp, whereas in TMM 41106-2778, it is smaller and located posterolingual to the main cusp. The anterior cingular cuspsule is barely discernible on the latter specimen.

The upper molars have the basic tribosphenic form modified by the addition of a prominent hypocone (except for M⁴) and by crown hypsodonty on the lingual side related to the protocone and hypocone. Also, they have a prom-

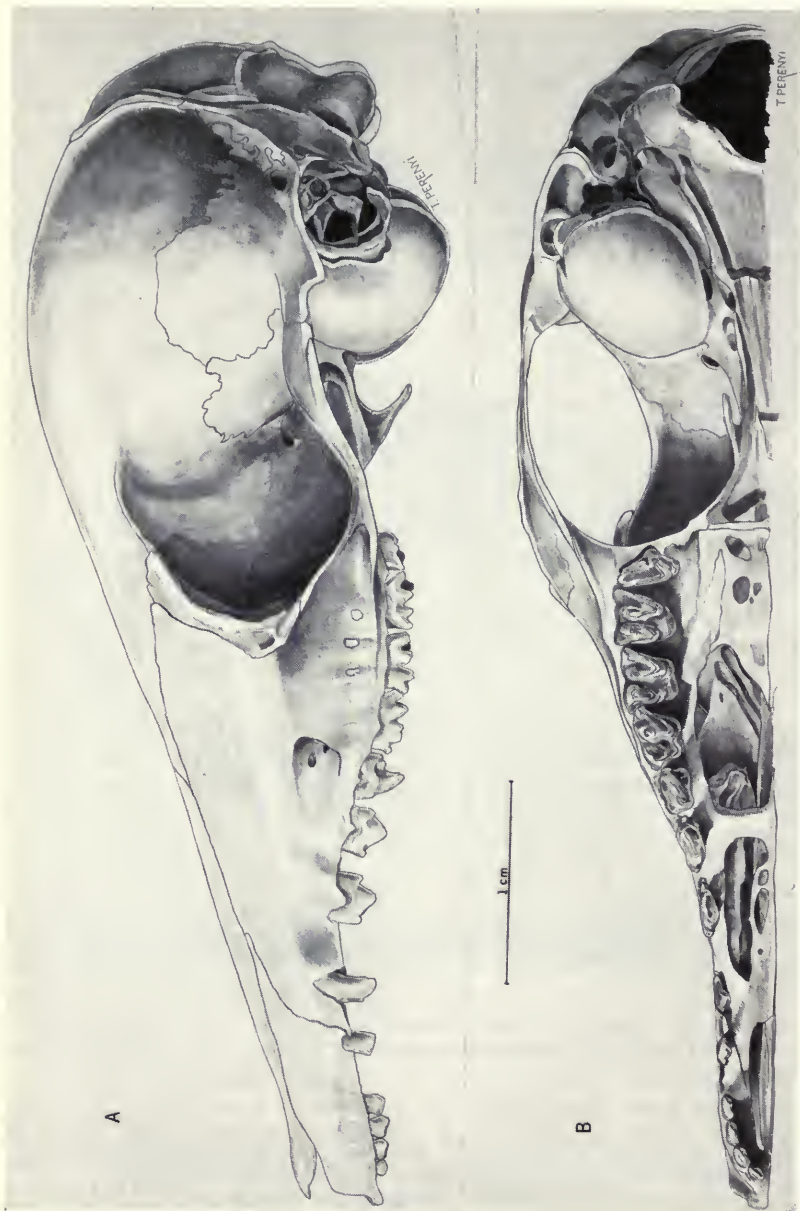


FIG. 2. *Perameles myosura notina* Thomas = *P. bougainvillei*. Specimen 9.2.181, Odontological Museum, Royal College of Surgeons, London. A & B, Left lateral and ventral views of the skull and its dentition.

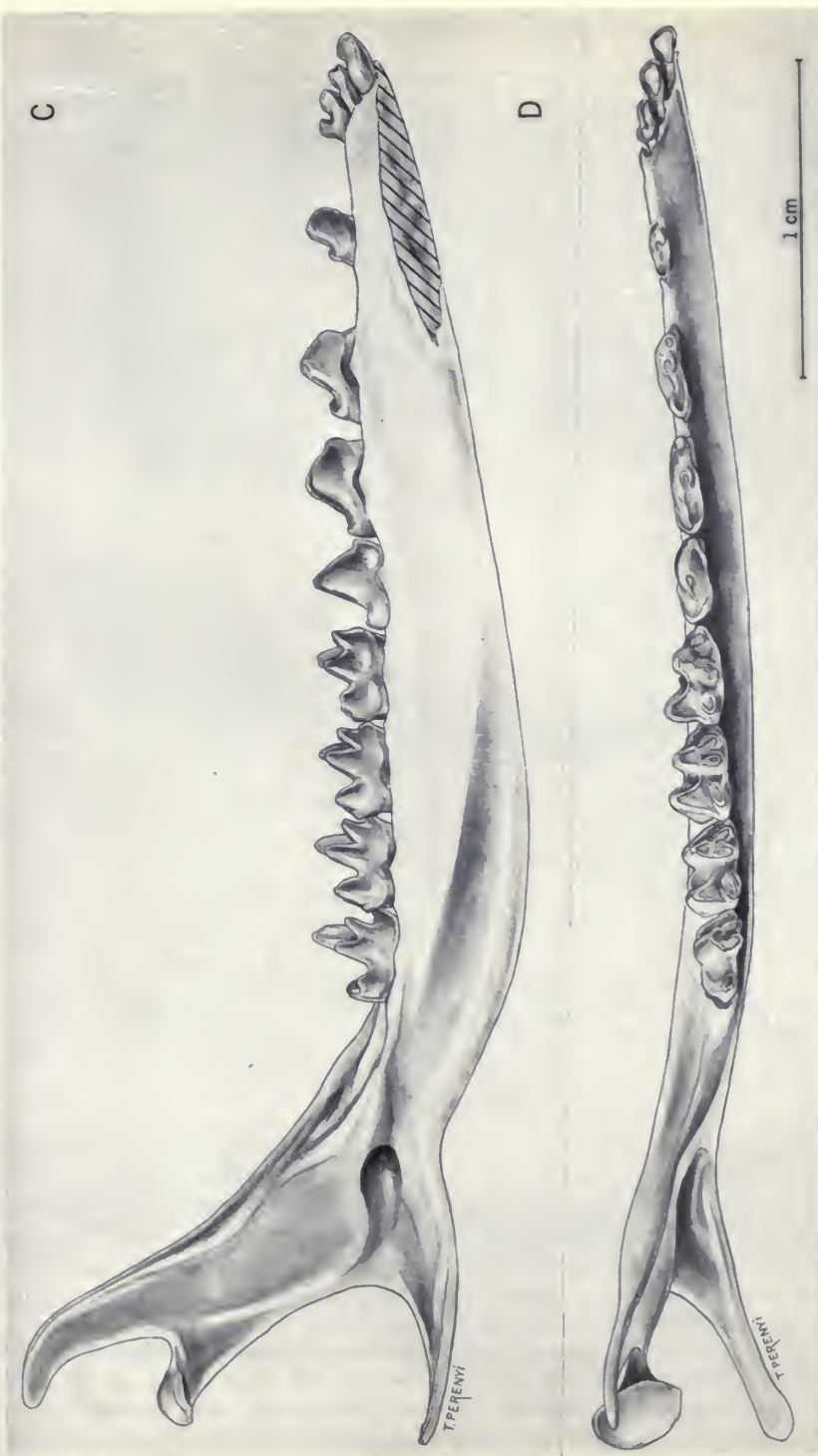


FIG. 2. C & D, Lingual and crown views of the left ramus and its dentition.

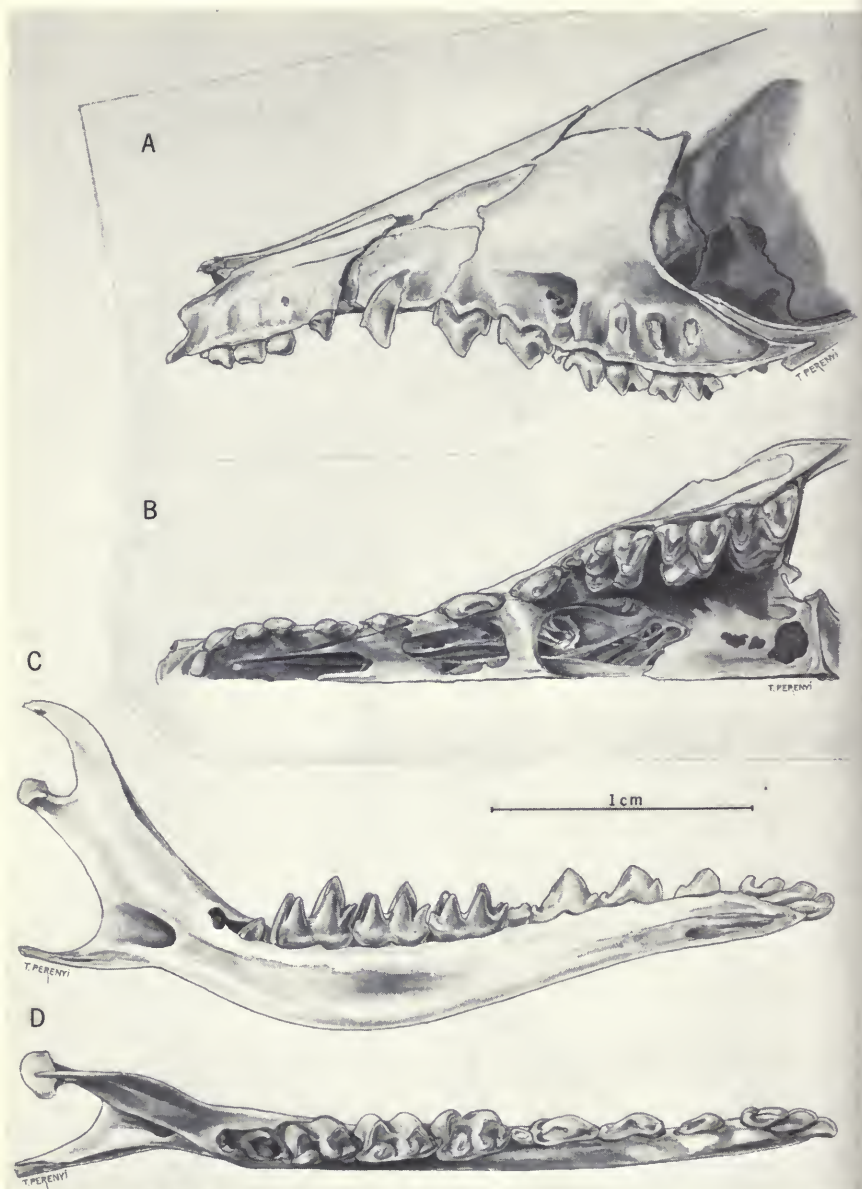


FIG. 3. *Perameles myosura notina* Thomas = *P. bougainvillei*. Specimen 9.2.182, a juvenile, Odontological Museum, Royal College of Surgeons, London. A & B, Left lateral and ventral views of the facial portion of the skull with its dentition. C & D, Lingual and crown views of the left ramus and its dentition.

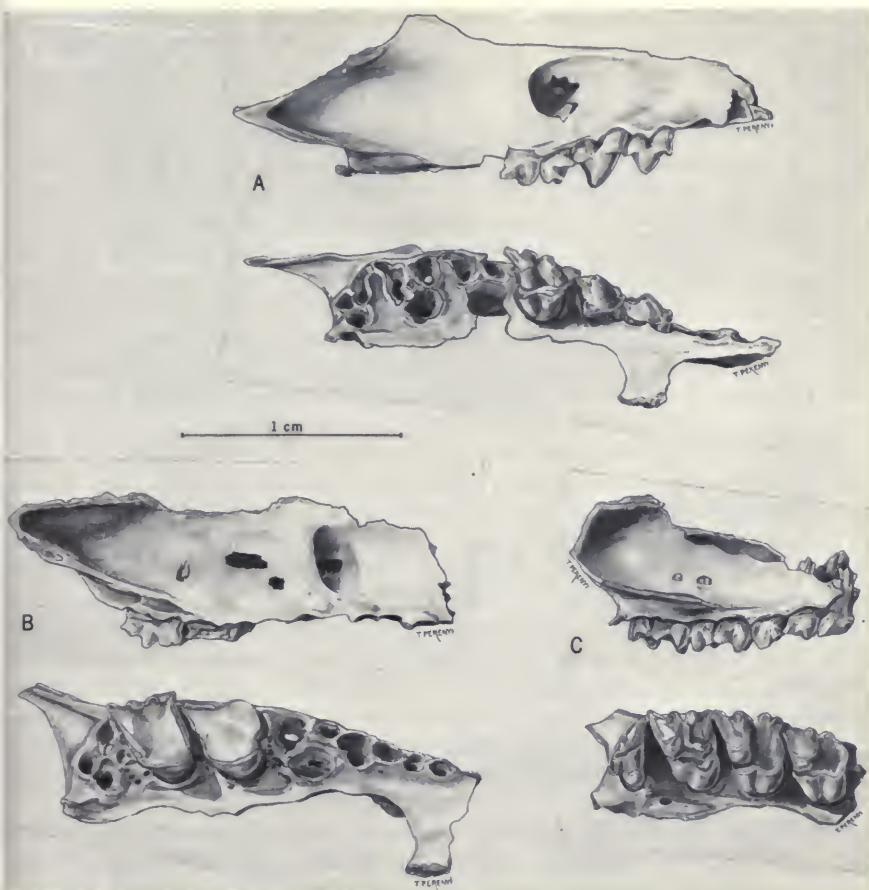


FIG. 4. *Perameles bougainvillei* from Madura Cave. A, TMM 41106-363, a right maxillary with P³-M¹ shown in lateral and crown views. Specimen is from Trench 3, Unit 2, Level 1. B, PM 13340, a right maxillary with M²⁻³ heavily worn, shown in lateral and crown views. Specimen is from Trench 3, Unit 2, Level 1. C, TMM 41106-512, a right maxillary fragment with all molars, shown in the same standard views. Specimen is from Trench 4, Unit 1, Level 1.

inent styler shelf with cusps that connect to the paracone (except M¹) and metacone (except M⁴) by crests so that a characteristically pinched, double V-shaped ectoloph results. They are all three-rooted teeth. Many of these crown features may be eroded by wear, and it is a common occurrence to find specimens in which all crown features are gone (fig. 4B).

The M¹ is approximately square in occlusal outline, with the parastyle and metastyle projecting anteriorly and posteriorly, respectively, along the labial edge. The metacone is the most prominent cusp, but it is not nearly as massive as the less prominent protocone. It is joined to the metastyle and to styler cusp 1 (ectostyle, see Hershkovitz, 1971) to form a prominent triangle. The paracone is usually joined only to cusp k and consequently it does not usually form the apex of a triangle. Rarely does M¹ have a weak crest to the parastyle. The protocone

and the hypocone are crescentic, and the protocone is the much larger of the two. The posterior crest of the hypocone extends around onto the posterior face of the metacone and rises towards the roots. A deep ectoflexus notch separates stylar cusps k and l.

The M^2 and M^3 are similar and will be described together. They both take the form of a truncated triangle in occlusal outline (fig. 4C), with the lingual side slightly shorter than the labial, although M^3 tends to be somewhat more triangular, with its linguallly bulging protocone and more reduced hypocone. The metacone is the most prominent cusp, and its relationship to the stylar cusps is the same as with M^1 . The paracone joins stylar cusp k and the parastyle by its crests. Protocone and hypocone are crescentic, the latter being much reduced in M^3 . Other differences between M^2 and M^3 are related to the positioning of the stylar cusps; the parastyle and metastyle being located farther labially with respect to cusps k and l in M^3 than in M^2 where all stylar cusps are in a straight line.

The M^4 is reduced, especially posteriorly (fig. 4C). It is a triangular tooth, the longest edge being the transversely oriented anterior one. The paracone, which is the largest cusp, is located near the lingual edge of the tooth and is connected to the parastyle by a long paracrista (I'). A short postparacrista—premetacrista (I'' a & b) or centrocrista (I''')—extends posteriorly from the paracone and turns abruptly linguad at the posterior end of the tooth. The labial edge of the stylar area is almost straight from the parastyle to the posterior end of the tooth where it too turns abruptly linguad and makes a hooklike projection. This posterior cusp at the junction of the back of the stylar shelf and the centrocrista (I''') could be a fused metacone-metastyle, but its homology is quite uncertain. Several small tubercles are present on the stylar shelf. The protocone is small and crescentic; its crests encircle the lingual part of the base of the paraconid.

Mandible.—The horizontal ramus of the mandible is slender (figs. 5-7). The ventral margin is convex beneath the molars and the P_4 and concave from there to the anterior end.¹ The dorsal edge of the horizontal ramus is twisted to the outside anteriorly. The symphysis is long, extending from the region of P_1 - P_3 to the anterior end of the ramus. The symphyseal area is concave, rugose, and has one prominent foramen. The lingual surface has a broad, shallow groove in the region underlying the molars. The major mental foramen is located under the P_2 . Other small foramina are variably located both anterior and posterior to the large one.

The ascending ramus rises at a low angle to the tooth row (less than 45°). Its anterior margin has a complex outline. Only the relatively short coronoid process rises steeply (at about 80°), and its tip is hooked posteriorly. The lower half of the ascending ramus is convex, and its upper half is concave. The masseteric fossa is narrow and has essentially the same width throughout its length. The posteroventral margin of the masseteric fossa is marked by a distinct ridge that parallels the anterodorsal margin. The ventral margin is broadened laterally to form a short shelf with a tubercle above the base of the angular process. The angular process tapers rapidly and evenly to a point. Its inner surface is concave.

The mandibular foramen lies in a broad depression above the anterior part of

¹In one specimen, TMM 41106-177 (fig. 6A, B), there is a prominent, pointed projection beneath P_3 , which is an abnormality that probably resulted from an injury.

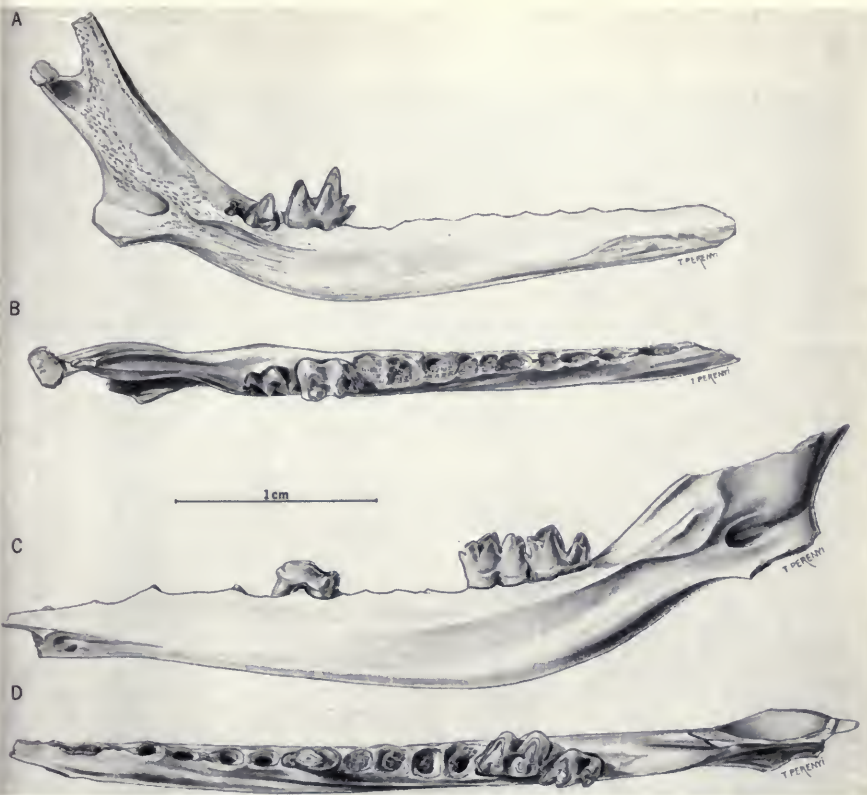


FIG. 5. *Perameles bougainvillei* from Madura Cave. A & B, TMM 41106-2771, a left mandible with M_{3-4} , alveoli of the rest of the dentition shown in lingual and crown views. Trench 4, Unit 2, Level 4. C & D, PM 27238, a right mandible with P_4 , M_{3-4} , and alveoli of the other teeth, shown in lingual and crown views. Trench 4, Unit 2, Level 1.

the base of the angular process. The medial surface of the ascending ramus is smooth and slightly convex.

The condyle is high with respect to the tooth row and is close to the coronoid process. Its articular surface is oval in outline but is slightly concave transversely and convex anteroposteriorly.

There are diastemata between I_3 and C, between C and P_1 , and a very short one between P_1 and P_3 . That between I_3 and C is usually ridged (sometimes double ridged) and sharp, and the ridge is turned labially. That between the C and P_1 is usually double ridged, but occasionally is only single ridged. The double ridges tie to the labial and lingual borders of the alveolus for the canine.

Lower dentitions.—No Madura Cave specimen has an incisor in place. There are a great many isolated incisor teeth, but we cannot be certain about their taxonomic assignments. A number of I_3 s that in the relatively unworn state are strikingly mitten-shaped most probably belong to this taxon because they compare closely with a sub-Recent specimen from Murraelellevan Cave (see figs. 1C, D; 2C, D; 3C, D). The alveolar pattern within the constricted anterior end of the



FIG. 6. *Perameles bougainvillei* from Madura Cave. A & B, TMM 41106-177, a left mandible with C, P₁ (or P₂), P₄, M₁, M₃₋₄, and alveoli of the other teeth, shown in the same standard views. Trench 3, Unit 2, Level 1. C & D, PM 27242, a right mandible with P₁ (or P₂), P₄, and M₃₋₄, alveoli of rest of the teeth, shown in the standard views. Trench 4, Unit 2, Level 1.

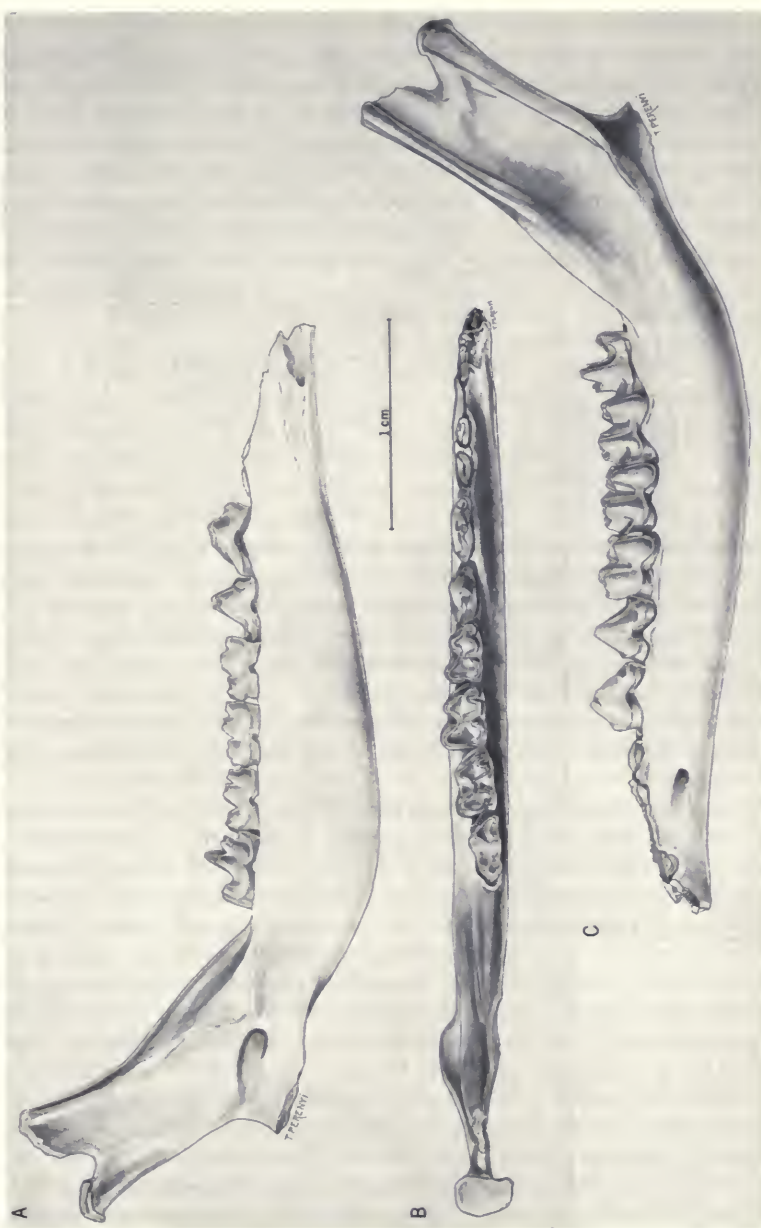


FIG. 7. *Perameles bougainvillei* from Madura Cave, TMM 41106-2753, a left mandible with P_3 - M_4 and alveoli or roots of the other teeth, shown in lingual (A), crown (B), and labial (C) views. Trench 3, Unit 2, Level 1.

horizontal ramus shows a pinched condition of the roots whereby I_2 is consistently squeezed up into a higher position than I_1 , which is always tight against the symphysis, and I_3 , which is low and farthest laterally for most of the length of its root.

The lower canine is relatively short anteroposteriorly, low, and very compressed laterally. The anterior edge is rounded, and there is no anterior cingular cuspule. The posterior edge is narrow but not sharp in the unworn state and terminates ventrally in a posterior cingular tubercle. Wear occurs at the top and dorso-posterolingual side of the tooth and results in shifting the posterior ridge labially. No sexual dimorphism is apparent, either in the few specimens with canine teeth in place or in the many jaws with empty canine alveoli. Measurements of maximum anterior-posterior length at crown-root junction (normal to ramus) for the only specimens with canines in place and for the associated alveoli are:

Specimens	Crown length (mm)	Alveolar length (mm)
WAM 75.1.19	2.43	3.65
TMM 41106-172	2.60	3.65
TMM 41106-177	2.43	3.50

The two anterior lower premolars, here designated P_1 and P_3 , are much alike. Each is double rooted, compressed laterally, and has its principal cusp located in the anterior half of the tooth and turned slightly lingually at its apex. They have anterior and posterior cingular cuspules. The anterior edge of the principal cusp of each is rounded, but the posterior edge has a thin sharp ridge in the unworn state. The posterior ridge that joins the posterior cuspule is rapidly modified by wear, most heavily on the lingual side of the posterior edge of the principal cusp. Both teeth have a faint posterior cingulum. The P_3 is the longest premolar.

The P_4 is approximately the same length as the P_3 but is less compressed laterally. Its principal cusp, which is located anterior to the mid-length, is relatively higher and wider than that of P_1 or P_3 . Its lingual surface is flat, but the labial surface is strongly convex. Like the P_1 and P_3 , the anterior edge of the principal cusp of P_4 is rounded, and the posterior edge is ridged. There are anterior and posterior cingular cuspules. The posterior one is joined by the ridge on the posterior edge of the principal cusp. A strong posterior cingulum extends over the posterior root on both sides. Wear rapidly removes the ridge on the posterior edge of the principal cusp, and in late wear stages the cusp is reduced to the level of those of P_1 and P_3 .

All of the lower molars have a slightly modified tribosphenic pattern, and with the exception of the M_1 are rather rectangular in crown view. All have tooth base hypsodonty (White, 1959) but to a lesser extent than in the other peramelids in the Madura Cave assemblage (*Isoodon*, *Chaeropus*, and *Macrotis*). It is strongest under the labial cusps. The paracristid and epicristid in all molars lack a carnassial notch.

The trigonid of the M_1 is distinctly narrower than the talonid, with a protoconid that has a more rounded, less protruding lingual outline. The other trigonid cusps are smaller and more tightly spaced than in the more posterior molars. The protoconid and metaconid of M_1 are the same size, but the pro-

toconid is slightly higher in an unworn tooth. The paraconid is smaller and lower than the others and shows no tendency to be laterally compressed as is the case in many dasyurids. The hypoconid and entoconid are the main cusps of the talonid. They are approximately the same height but are differently shaped. The entoconid is circular in cross section when unworn and is not connected to any other cusp. It has an upstanding, high conical shape initially, and wear on its labial surface alters the cross section to an oval shape. The hypoconid is crescentic and is connected to the posterolingual part of the base of the protoconid and to the hypoconulid. The hypoconulid is low and projects backward. There is no posterior cingulum and usually only a trace of an anterior one. Sometimes the anterior cingulum is distinct but small, sometimes absent. A small cingulum occupies the notch between protoconid and hypoconid near the base of the former.

The M_2 and M_3 are similar in size and morphology. Both have a trigonid that is wider than long, as a result of the far lingual placement of the protoconid and the closely spaced paraconid and metaconid. The protoconid and metaconid are equal in size and height; the paraconid is smaller. The talonid of both M_2 and M_3 is like that of M_1 in size and arrangement of the hypoconid and entoconid. The hypoconulid of M_2 is smaller than that of the M_1 , and that of M_3 is virtually gone. In M_2 , the posterior crest of the hypoconid joins the hypoconulid as in the M_1 . In the M_3 , this crest either joins the vestige of the hypoconulid or it disappears at the posterior side of the entoconid. Both teeth lack a posterior cingulum, and each has the small labial one between protoconid and hypoconid. The M_2 and M_3 differ from one another and from M_1 and M_4 in the size of the anterior cingulum. It is weakest on M_1 and becomes progressively larger toward M_4 . The trigonid of the M_2 is narrower than that of the M_3 . This character, which is easily observed in specimens with the teeth in jaws, is of little use in distinguishing isolated M_2 s and M_3 s because the variations in absolute size and extent of wear are great enough to cause broad overlap of measurements.

The M_4 resembles the M_2 and M_3 in the arrangement of its cusps, but it is narrower, and the relative sizes are different. The protoconid is the largest cusp, and the paraconid and metaconid are equal in size. The talonid is reduced in comparison with the other molars. A distinct basin is bordered by a tall conical entoconid and a crescentic hypoconid, the crests of which go to the anterior and posterior sides of the base of the entoconid. No hypoconulid is present. As a result of the failure of the cristid obliqua to join the epicristid, the talonid basin is joined to the trigonid only by the hypoflexid at the lingual edge of the tooth. The area labial to the hypoflexid slopes downward labially into another basin that is bordered labially by the cingulum that joins the protoconid and hypoconid.

Fossil bandicoots lose their teeth more readily than most other mammals. Hence, a high proportion of isolated teeth is encountered. The more distinctive first and last molars cause no problems of identity, but M_2 s and M_3 s are so similar to one another (as are M_2 s and M_3 s) that their separation is far less certain when they are recovered as isolates. The M_2 s can be distinguished from M_3 s most of the time by the more nearly equal-sized protocone and hypocone; also the M_3 has a smaller hypocone than the M_2 . The styler cusps of the M_2 s tend to be arranged in a straight line, whereas in the M_3 s the parastyle and metastyle tend to be located labial to styler cusps k and l. Standard measurements fail to separate the M_2 s and M_3 s (fig. 8).

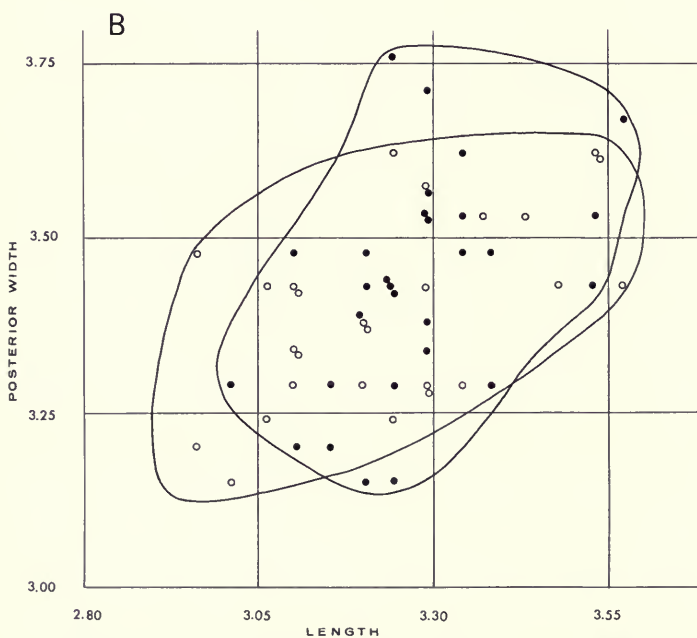
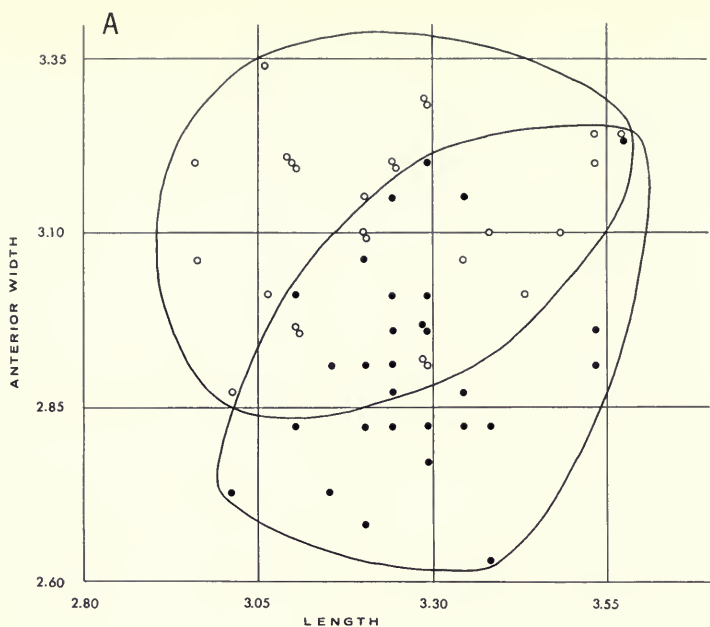


FIG. 8. Bivariate graphs of the cheek teeth of *Perameles bougainvillei*. **A & B**, Plots of length vs. anterior width and length vs. posterior width, showing extensive overlap of M²s and M³s. Initial determination based on visual criteria. All are from Trench 4, Units 4-5. Dots indicate M²s, circles M³s. Measurements are in millimeters.

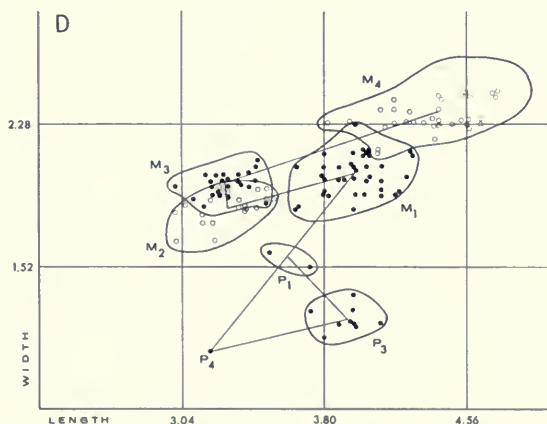
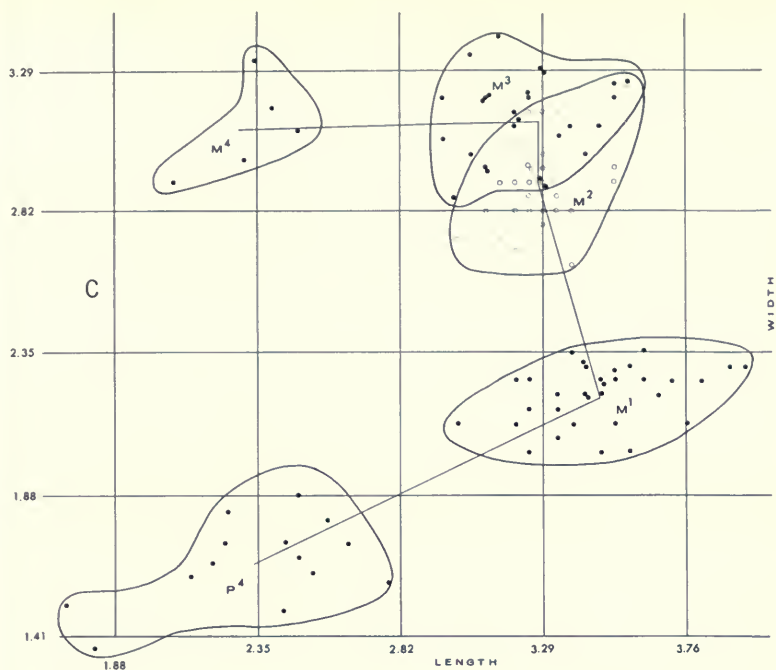


FIG. 8. C & D, Length vs. width plots of tooth measures for identified cheek teeth from Madura Cave. Means for each adjacent tooth are connected to form a pattern. In C, the upper cheek teeth are shown, in D, the lowers. For the premolars, the ordinate measure is the greatest width perpendicular to tooth length; for the molars, it is anterior width.

In crown view, the M2s differ from the M3s in having talonids that are relatively wider than the trigonids. Scatter diagrams of length versus anterior width and length versus posterior width show no separation (fig. 9B, C), but scatter diagrams of anterior width versus posterior width and length versus AW/PW confirm the visual observation, although the clouds of points almost touch (fig. 9A, D).

DISCUSSION

Perameles bougainvillei (following Tate, 1948, and Wakefield, 1966, including *P. myosura*, *P. fasciata*, *P. notina*, and *P. eremiana*) is widely distributed through the drier parts of southern and western Australia (Shortridge, 1909; Jones, 1924; Troughton, 1962; Marlow, 1962; Freedman, 1967; Ride, 1970; Brooker, 1977). Abundant remains of *P. bougainvillei* that are found in surface deposits of caves

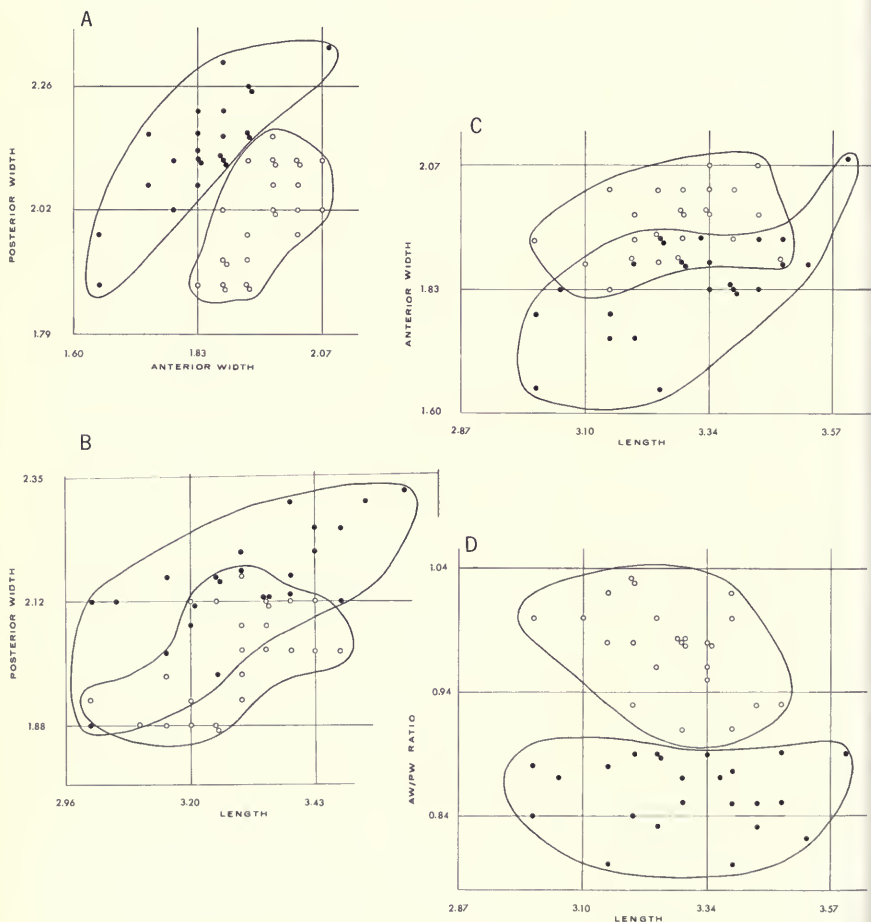


FIG. 9. Bivariate graphs of isolated M2s and M3s of *Perameles bougainvillei*. Initial determination based on visual (proportion) criteria. M2s shown by dots, M3s by circles. In A and D, complete separation is shown; in B and C, overlap.

on the Nullarbor Plain attest to its Pleistocene and Recent occupancy of this region. On the basis of means of dental measures, the Madura Cave populations are closer to the Recent South Australian *P. b. notina* sample analyzed by Freedman and Joffe (1967) than to the Recent *P. b. bougainvillei* sample from Bernier and Dorre Islands.

Perameles bougainvillei is found in abundance throughout the stratigraphic sequence at Madura Cave. A comparison of qualitative characters of samples from units 1 and 4-5 shows no apparent differences. It might be expected that the Pleistocene representatives of the species would be larger than those of Holocene age, as is the case with many mammals (Marshall, 1974; Marshall & Corruccini, 1978). A comparison of means for pairs of measures (tables 1, 2) shows that in most instances those of the samples from unit 4-5 are indeed larger than those from unit 1. One-sided "t" tests on nine sets of dental measures show significant differences in three cases (table 3). However, a sign test (Siegel, 1956, p. 68) for directionality of the differences of the means gives an insignificant result ($P = .090$ for a one-sided test). Clearly this is a borderline situation in which the differences between the materials from these two units are slight.

Smith (1972, p. 128, table 5) shows that a Pleistocene sample of *P. bougainvillei* from Victoria Cave in South Australia tends to have larger means than those of a Holocene sample from Fromm's Landing (also in South Australia; Wakefield, 1964). In this parallel case, four out of 13 one-sided "t" tests are significant (table 4). Here a sign test gives a significant result ($P = .046$ for a one-tailed test).

TABLE 1. Numerical data on some dental measurements of *Perameles bougainvillei* from units 1 and 2 of Madura Cave.

Variate	Sample size	Observed range	Mean \pm standard error	Standard deviation	Coefficient of variation (%)
Unit 1					
M ¹ L	10	3.24-3.76	3.48 \pm .054	0.172	4.92
AW	9	2.05-2.66	2.35 \pm .070	0.210	8.94
PW	9	2.82-3.47	3.16 \pm .066	0.198	6.25
M ² L	9	3.07-3.38	3.21 \pm .038	0.117	3.58
AW	9	2.67-3.06	2.89 \pm .054	0.161	5.56
PW	9	3.20-3.62	3.37 \pm .041	0.123	3.60
M ³ L	4	2.91-3.20	3.07	0.129	
AW	5	2.98-3.20	3.11	0.102	
PW	4	3.29-3.38	3.34	0.038	
M ⁴ L	2	2.44-2.82	2.63		
AW	2	2.92-3.24	3.08		
PW	2	1.55-1.83	1.69		
Unit 2					
M ₁ L	2	2.82-2.85	2.84		
AW	2	1.44-1.64	1.54		
PW	2	1.94-2.07	2.01		
M ₂ L	3	2.94-3.29	3.14	0.169	
AW	3	1.82-1.93	1.88	0.047	
PW	3	2.18-2.28	2.23	0.047	
M ₃ L	3	2.89-3.29	3.09	0.200	
AW	3	1.82-2.03	1.91	0.108	
PW	3	2.03-2.18	2.10	0.076	

TABLE 2. Numerical data on some dental measurements of *Perameles bougainvillei* from units 4-5 of Madura Cave.

Variate	Sample size	Observed range	Mean \pm standard error	Standard deviation	Coefficient of variation (%)
M ¹ L	32	3.01-3.95	3.48 \pm .037	0.211	6.05
AW	32	2.02-2.35	2.21 \pm .017	0.096	4.34
PW	32	2.30-2.68	2.53 \pm .019	0.109	4.32
M ² L	29	2.78-3.57	3.19 \pm .034	0.181	5.67
AW	29	2.65-3.24	2.91 \pm .028	0.151	5.17
PW	29	3.15-3.76	3.43 \pm .030	0.159	4.63
M ³ L	26	2.95-3.57	3.23 \pm .035	0.177	5.48
AW	26	2.91-3.34	3.12 \pm .025	0.128	4.11
PW	26	3.15-3.62	3.39 \pm .026	0.133	3.90
M ₂ L	23	3.01-3.62	3.30 \pm .034	0.163	4.93
AW	23	1.64-2.07	1.84 \pm .020	0.094	5.10
PW	23	1.86-2.35	2.15 \pm .022	0.107	4.99
M ₃ L	24	3.01-3.48	3.28 \pm .023	0.111	3.40
AW	24	1.86-2.07	1.96 \pm .013	0.065	3.31
PW	24	1.86-2.16	2.01 \pm .019	0.094	4.69

TABLE 3. Results of "t" tests of some dental measurements of *Perameles bougainvillei* from units 1 and 4-5 of Madura Cave.

Measurement	"t"	Degrees of freedom	Probability (one-sided test)
M ¹ L
AW	2.900	39	P < .005*
PW	12.628	39	P < .001*
M ² L	.310	36	.35 < P < .40
AW	.342	36	.35 < P < .40
PW	1.036	36	P > .15
M ³ L	1.726	28	P < .05*
AW	.164	29	.40 < P < .45
PW	.737	28	.20 < P < .25

*Significant at .05 level.

**Means identical.

TABLE 4. Results of "t" tests on means of some mandibular and dental measurements of *Perameles bougainvillei* from Victoria Cave, South Australia, and Fromm's Landing, South Australia (based on data from Smith, 1972, table 5).

Measurement	"t"	Degrees of freedom	Probability (one-sided test)
Length M ¹⁻⁴	2.497	6	P < .025*
Length ascending ramus	1.883	32	.05 > P > .025*
Mandible breadth at M ₂	1.263	41	.15 > P > .10
Mandible height at M ₂	0.741	38	.25 > P > .20
P ₄ L	0.768	11	.25 > P > .20
M ₁ L	0.067	5	P > .9
PW	2.473	6	.05 > P > .025*
M ₂ L	3.875	11	.005 > P > .0005*
PW	1.420	10	.1 > P > .05

TABLE 4. *Continued*

Measurement	"t"	Degrees of freedom	Probability (one-sided test)
M ₃ L	0.559	14	.30 > P > .25
PW	0.737	14	.25 > P > .20
M ₄ L	1.364	15	.1 > P > .05
PW	0.131	15	.45 > P > .40

*Significant at .05 level.

Both of these situations indicate a post-Pleistocene reduction in size in *Perameles bougainvillei*, although the magnitude of the change was less than that reported for larger animals (Marshall & Corruccini, 1978).

Isoodon Desmarest, 1817

Isoodon obesulus (Shaw and Nodder, 1797)

MATERIAL

Trench 2, 2½ ft

PM 25224, left ramus with M₃ and alveoli of P₄-M₂ and M₄ (fig. 11G)

Trench 4, Unit 1, top 1 ft

TMM 41106-568, fragment of upper molar

TMM 41106-669, right M³

TMM 41106-672, left M² (fig. 11B)

TMM 41106-673, left M³ (fig. 11D)

TMM 41106-675, left M₂

TMM 41106-677, right M₂ or ₃

WAM 75.1.124, left maxillary fragment with M³

PM 26331, left ramus fragment with M₄, juvenile

PM 26362, very worn lower molar, probably M₁

Trench 4, Unit 2, Level 1

TMM 41106-708, right M³ or ²

Trench 4, Unit 2, Level 2

TMM 41106-705, left M¹ (fig. 11A)

TMM 41106-706, left M₂ or ₃

TMM 41106-710, left M²

TMM-41106-711, right M³

TMM-41106-712, left M² or ³

PM 26307, left M₁ (fig. 11F)

PM 26334, left ramus with M₄ and condyle (fig. 11H)

Trench 4, Units 4-5

TMM 41106-709, right M²

TMM 41106-714, right M₂ or ₃

TMM 41106-715-6, two right M¹s

TMM 41106-717, 19-20, three right M³s

TMM 41106-721, right M³ (fig. 11C)

TMM 41106-722, left M³

TMM 41106-723, left M²

Trench 4, Units 4-5 (continued)

- TMM 41106-724, left M² or 3
- TMM 41106-725, left M²
- TMM 41106-726, left M² or 3
- TMM 41106-727, left M²
- WAM 75.1.125, left M₂ or 3
- PM 26308, left M₂ or 3
- PM 26309, talonid of a left lower molar
- PM 26310, right M₂ or 3
- PM 26311, left M₂ or 3
- PM 26312, right M₄
- PM 26313, left M₄ (fig. 11I)
- PM 26314, left M²
- PM 26315, fragment of left M² or 3
- PM 26316, right M¹
- PM 26317, left M² or 3
- PM 26320-3, four right M₁s
- PM 26324, left M² or 3
- PM 26325, left M₃
- PM 26326, right M²
- PM 26327, left M₄
- PM 26328, left lower molar
- PM 26329, left M₂
- PM 26962, left M⁴ (fig. 11E)
- PM 27740, left M₂ or 3
- PM 30552, edentulous right ramus
- PM 33660-2, three left M¹s

Trench 5, Unit 5

- WAM 75.1.126-7, two broken right lower molars

DESCRIPTIONS

Upper molars.—The upper molars have all the characters seen in extant specimens of *Isodon obesulus* (fig. 10A-C). The first through the third molars are nearly square in occlusal view with moderate tooth base hypsodonty (White, 1959), especially in that part of the tooth that supports the protocone and hypocone. As with most peramelids, the labial part of the tooth is offset from the lingual part so that it extends farther ventrally (or where seen in palatal view appears to be raised above the lingual side).

The M¹ (fig. 11A, TMM 41106-705) is slightly rectangular in occlusal view. The anterior end is somewhat narrower than the posterior end. The wear facets indicate that the protocone is slightly taller than the hypocone in an unworn tooth, although wear rapidly brings them to the same level. They are joined at a higher level than the central basin. The protocone merges with an anterior lingual cingulum that extends across the anterior face of the tooth and nearly joins a smaller cingulum from the parastyle. A similar but larger postcingular ridge extends from the hypocone across the posterior face of the tooth nearly to the posterolabial corner.

The paracone is joined to the weak stylocone by a curved ridge that extends on to cusp k. The ridge joining the paracone and parastyle is sometimes faintly visible on the anterior face of the paracone (TMM 41106-705, -716, and PM 26316). The parastyle is much smaller than in the posterior molars. The metacone is joined to the anterolingual base of the mesostyle and to the metastyle to form a triangle as in M^2 and M^3 . A smaller styler cusp is present anterior to the metastyle in TMM 41106-705, -715, but is absent in -716 and PM 26316 (probably as a result of wear in the latter). The metastyle is located farther posterolabially than in most specimens of M^2 and M^3 . In all of these features, the Madura Cave specimens conform to the comparative specimens available to us [TMM M-851, FMNH 98899 (fig. 10A, B), both Recent specimens; and PM 25506, -7, and -9, all Pleistocene to post-Pleistocene specimens from caves in the Margaret River area of Western Australia].

The M^2 and M^3 of *I. obesulus* are so alike that separation of isolated teeth is uncertain. They either lack a stylocone or have only a weakly developed one. They are square in contrast to those of *Perameles*, in which the labial edge is longer than the lingual edge (fig. 11B, C; TMM 41106-672, an M^2 ; and -721, an M^3).

The protocone and hypocone are crescentic when unworn and are joined above the level of the central basin. The protocone is slightly higher than the hypocone. In some specimens (TMM 41106-673, -709, -710, and -721), a low, indistinct ridge extends from the junction of the protocone and hypocone into the central basin where it disappears. This area of the tooth is flat in the other Madura fossils and in our comparative specimens. A ridge extends anteriorly from the protocone for a variable distance around the paracone. It disappears on the anterior face of the tooth near the base of the parastyle in TMM 41106-669 and -672. In TMM 41106-673 (fig. 11D) and -719, it joins the parastyle. A similar ridge usually extends posteriorly from the hypocone around the metacone almost to the posterolabial corner of the tooth. In TMM 41106-669, -712, and -720, this ridge disappears about halfway across the posterior face of the tooth.

The labial two-thirds of the occlusal surface is occupied by two triangles whose apices are the paracone and metacone. The paracone is not as tall as the metacone and is joined to the apex of the parastyle and the base of cusp k by the eocrista ($I'y$ and $I'''a$, respectively). Cusp k has a crest that extends toward crest $I'y$ in TMM 41106-673. It meets and joins a very weak crest from $I'y$ in the intervening valley. The metacone is joined to the base of the mesostyle (the cusp lettered l) by the crista ($I'''b$) and to the apex of the metastyle by a crista (I''). A small styler cusp (m) is present anterior to the metastyle.

Cusp k and the mesostyle (l) are approximately the same size, are larger than the parastyle and metastyle, and are weakly connected at their base. Cusp k is oval in cross section, and the mesostyle (l) is circular.

In an attempt to find a way of distinguishing M^2 s from M^3 s, and M^2 s from M^3 s, a number of bivariate graphs were drawn, based upon the usual dental measures, none of which gave plots without some degree of overlap of the clouds of points. Figure 12 shows two of these in which length vs. anterior width are plotted for four small samples of Recent and fossil specimens of *I. obesulus*. The most successful plot is shown in (A) wherein M^2 s and M^3 s can be separated about three-fourths of the time. The sort of plot shown in (B) for the same measures for the lower teeth is more typical, however, and illustrates the

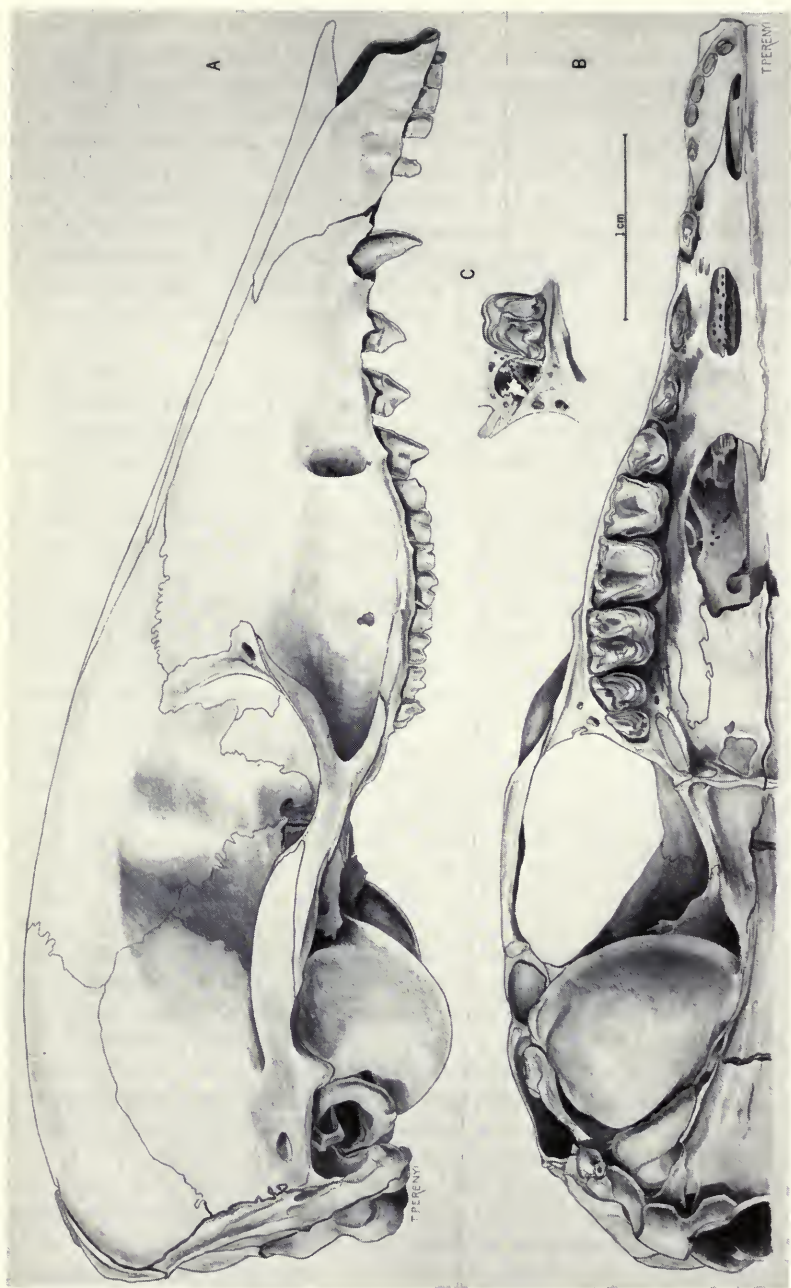


FIG. 10. *Isodon obesulus affinis* (Waterhouse), FMNH 98899, from Wynyard, Tasmania. A & B, Right lateral and ventral views of the skull and its dentition. Note the aberrant condition shown by this individual; on the right side there are five molars, whereas on the left the usual four were present, C shows M^3 in place, and the alveoli of M^4 indicate the normal molar count for the left side.

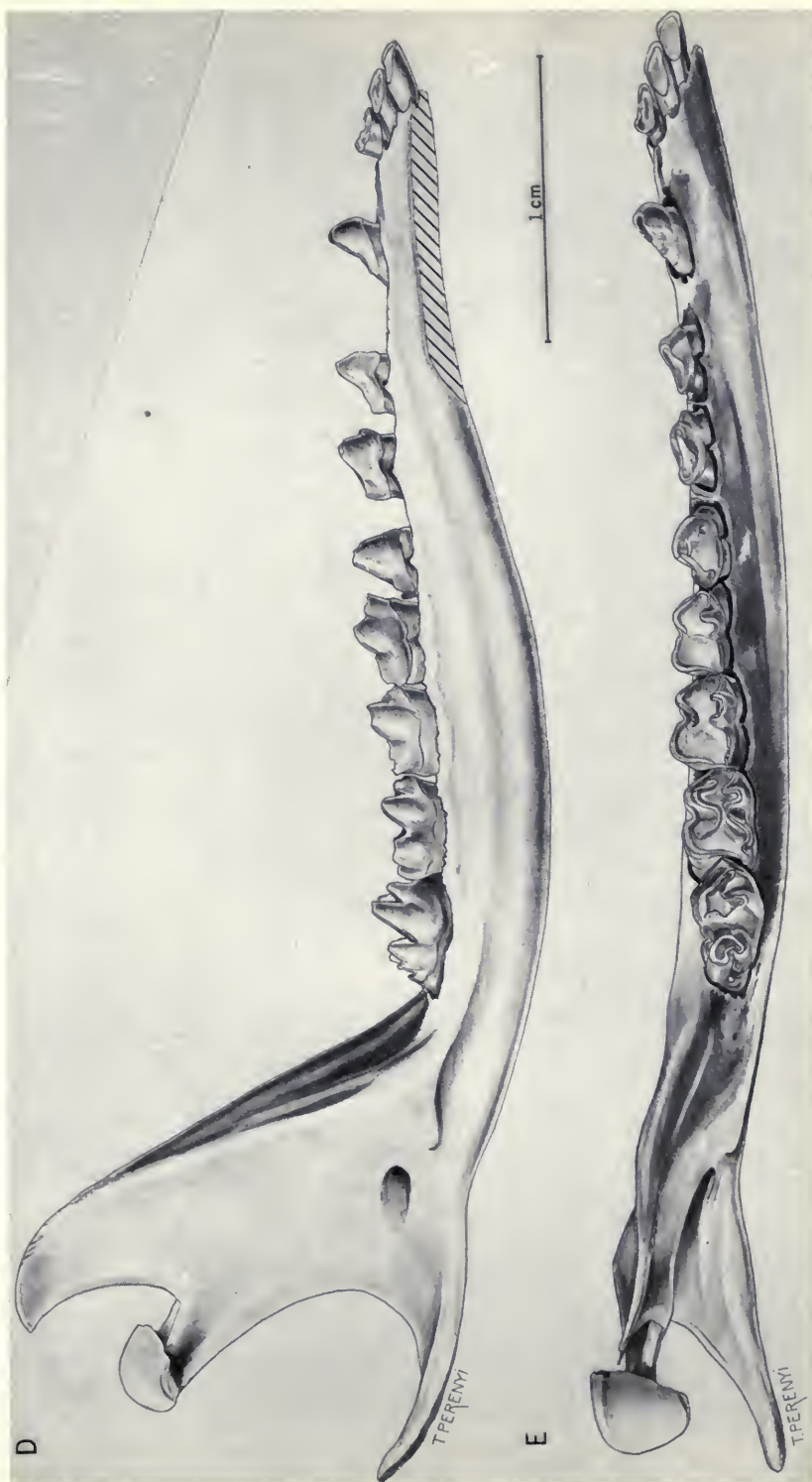
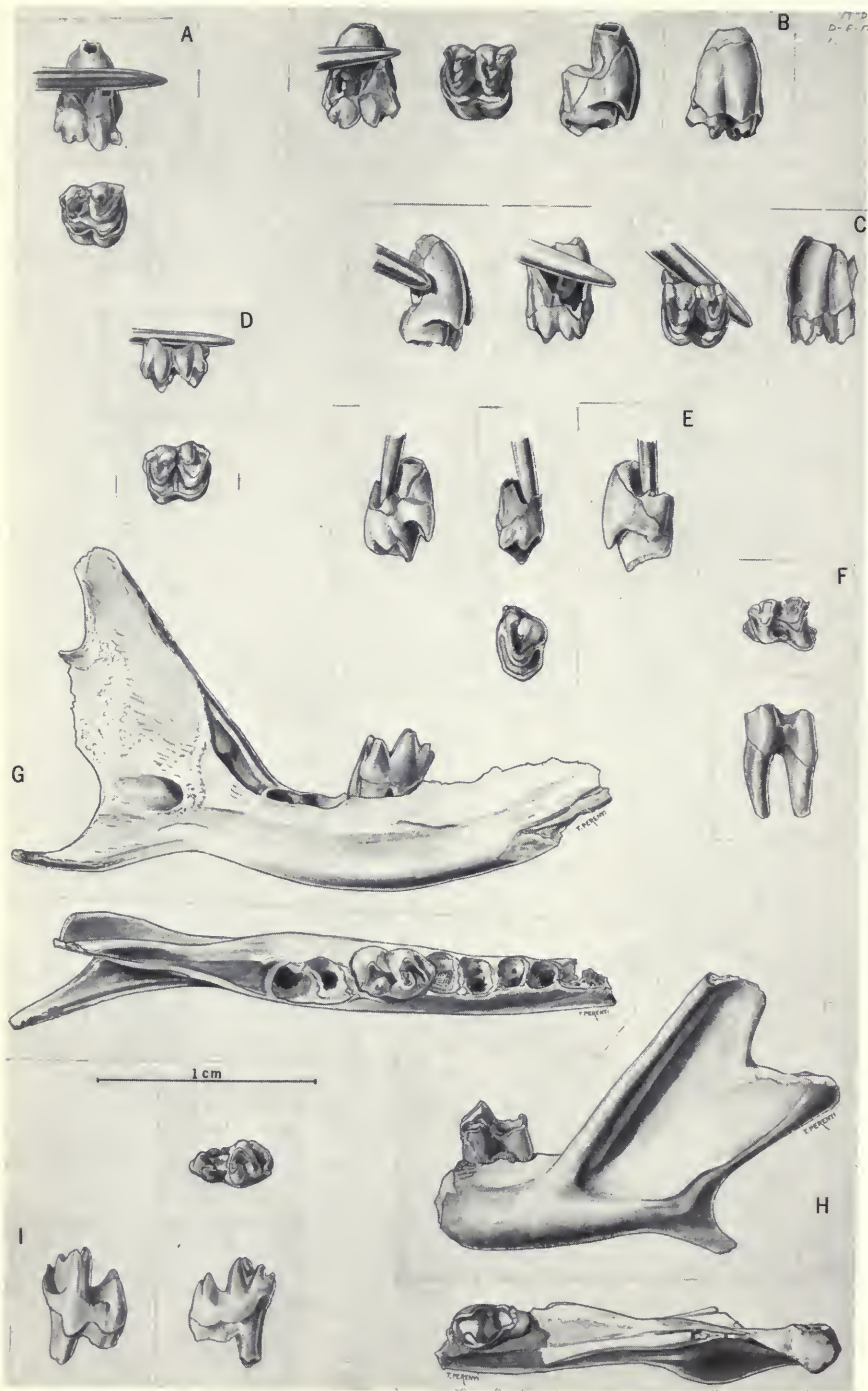


FIG 10. D & E, Lingual and occlusal views of the left mandible and its dentition. On both sides, the lower tooth count is normal.



need to find some discrete features or other kinds of dental measures than these standard ones if positive separations are to be achieved. Similar results were obtained with the Madura Cave teeth (fig. 13).

The M^4 differs from the other upper molars in the extreme reduction of the posterior cusps (fig. 11E; PM 26962). It is ovoid in occlusal view. There are three principal cusps—protocone, paracone, and cusp k. The paracone and protocone are crescentic cusps with prominent anterior and posterior ridges. Those of the paracone both reach the labial edge of the tooth. The anterior one joins a small, indistinct stylocone-parastyle at the labial edge of the tooth. The posterior ridge of the protocone reaches the labial edge of the tooth, but the anterior one does not. Cusp k is a conical cusp that is situated on the labial edge of the tooth between the ends of the ridges of the paracone. There is no trace of a posterior cusp, unlike the situation in most of the Recent specimens we have examined, which have a small posterolabial cusp.

Mandible.—Three partial mandibles of *Isodon* are present in the Madura Cave collection. All represent the posterior part of the mandible. The horizontal ramus is slender and relatively shallower than that of dasyurids of comparable size. It is deeper and wider than that of *Perameles*. The angular process is directed inward and posteriorly, is broad basally, and tapers rapidly to a slender termination. The mandibular foramen is located above the anterior part of the base of the angular process.

The ascending ramus is broad. Its anterior border rises steeply, forming an angle of more than 45° with the line of the tooth row (fig. 11G, PM 25224). In this character, *Isodon* resembles the dasyurines, *Chaeropus* and *Macrotis*, and differs from *Perameles* in which this angle is less than 45° , and the masseteric fossa is narrow. The ventral margin of the masseteric fossa is marked by a prominent shelf that is expanded laterally over the base of the angular process.

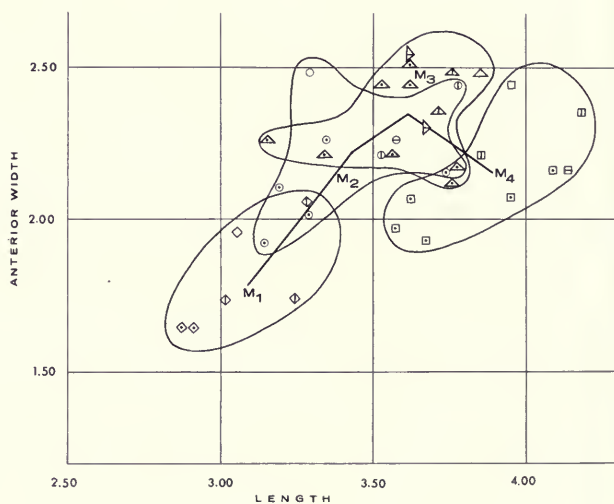
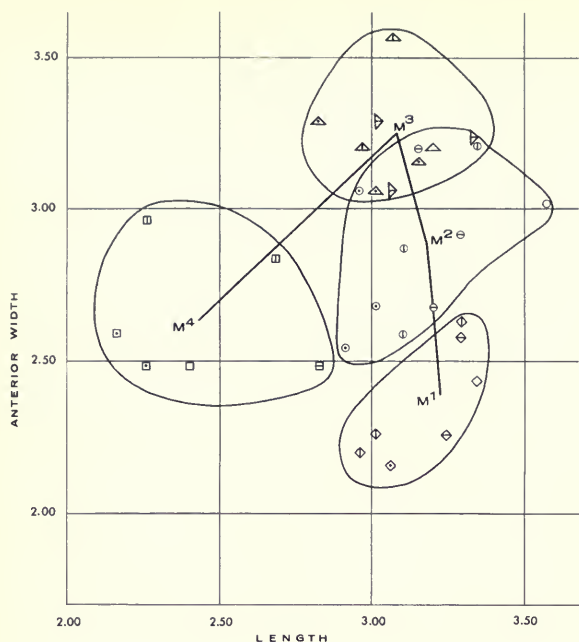
The condyle is located closer to the coronoid process than to the angular process. The articular surface of the condyle is broadly oval in outline (fig. 11H; PM 26334). It has no curvature transversely but is gently convex antero-posteriorly.

Lower molars.—All lower molars have well-developed trigonids but lack carnassial notches on the major crests. They have tooth base hypsodonty especially beneath the hypoconid. The trigonid is higher than the talonid on all molars.

The M_1 is an elongate tooth that tapers anteriorly (fig. 11F; PM 26307). The trigonid is distinct but relatively smaller than in M_2 - M_{2-4} . The protoconid and metaconid are subequal, and the paraconid is distinctly smaller and lower. There is no anterior cingulum, but there is a slight concavity (on the anterolateral side of the tooth) between the protoconid and paraconid.

Opposite:

FIG. 11. *Isodon obesulus* from Madura Cave. A, Crown and labial views of TMM 41106-705, a left M^1 . B, Labial, crown, distal (posterior), and lingual views of TMM 41106-672, a left M^2 . C, Proximal (anterior), labial, crown, and lingual (inverted) views of TMM 41106-721, a right M^3 . D, Crown and labial views of TMM 41106-673, a right M^3 . E, Distal, lingual, proximal, and crown views of PM 26962, a left M^4 . F, Crown and labial views of PM 26307, a left M_1 . G, Lingual and dorsal views of PM 25224, a left ramus with M_3 , and alveoli of P_4 - M_2 and M_4 . H, Labial and dorsal views of PM 26334, a left ramus fragment with M_4 . I, Crown, labial, and lingual views of PM 26313, a left M_4 .



	M ₁ ¹	M ₂ ²	M ₃ ³	M ₄ ⁴
RECENT TASMANIA	◇	○	△	□
RECENT SW. AUSTRALIA	◊	⊙	▴	▣
FOSSIL SW. AUSTRALIA	◊	⊙	▴	▣
HASTING'S CAVE	◇	○	△	□

FIG. 12. Bivariate graphs of length vs. anterior width measurements of upper and lower molars of Recent and fossil specimens of *Isodon obesulus*. In A, the bivariate plots for the upper molars show a clear separation for M₁'s and M₄'s, but only a partial separation between M₂'s and M₃'s. In B, similar plots for the lower molars show extensive overlap between adjacent teeth. Straight lines connect the midpoints of the plots for adjacent teeth. Measurements are in millimeters.

The talonid is broader than the trigonid. The entoconid is the highest cusp. It is subconical in shape and occupies almost all of the lingual edge of the talonid. The hypoconid is slightly lower than the entoconid but is more massive because of the underlying tooth base hypsodonty. The hypoconulid is the smallest of all the cusps and the most subject to erasure by wear. In an unworn or little-worn tooth, it projects posteriorly behind the entoconid in line with all the other lingual cusps.

The hypoconid is tapered toward its apex so that in an unworn or little-worn tooth its crests make a tight V. With wear, this V becomes more open. The cristid obliqua ($I''b$) connects the hypoconid to the midpoint of the base of the epicristid (II) of the trigonid. The postmetacristid (I') connects the hypoconid to the hypoconulid. In an unworn tooth, this ridge has a slight posterior curvature but becomes straight with wear.

There is a small cingulum in the reentrant between the protoconid and hypoconid. It may bear a small cuspule. In an unworn specimen, this cingulum is located halfway between the top of the cristid obliqua and the enamel line between the roots.

The M_2 and M_3 are so similar in both size and morphology (fig. 11G) that they cannot be reliably separated and are therefore treated together. Both are similar to the M_1 in general morphology. They can be distinguished from the M_1 by the presence of a prominent bulging anterolabial cingulum, a more massive trigonid, and larger size. The most consistent difference between M_2 and M_3 seems to be the degree of development of the hypoconulid: larger on M_2 than M_3 . Since this feature is reduced by wear, it is best seen in unworn specimens (PM 26325, 26329). Recent specimens with all teeth in place show a gradual decrease in development of the hypoconulid from M_1 through M_3 . The lingual cusps of the M_2 and the M_3 do not fall on a straight line as they do in *Perameles*, but form a curved line, with the paraconid and hypoconulid located labial to the metaconid and entoconid.

The M_4 differs from the M_{2-3} primarily on the structure of the talonid and its slightly greater length. The trigonid of the M_4 has the same construction as that of the M_{2-3} but is slightly more massive (fig. 11H, I; PM 26334 and PM 26313). The talonid is elongate but is otherwise reduced. The hypoconid and entoconid are the two principal cusps. The entoconid is higher, but the hypoconid is more massive and crescentic. The connection to the trigonid is variable, ranging from no ridge through a broad, rounded ridge, to a weakly developed, but sharp, ridge. The hypoconulid may be present or absent. Where present, it is small and below the notch between the hypoconid and entoconid. The cingulum between the protoconid and hypoconid is larger than on the other molars. It has a variable number of cuspules and isolates a small basin.

Comparisons.—A comparison of the Madura Cave specimens with Recent and fossil specimens from southwestern Australia shows them to be similar in morphology but different in size (table 5). The means of the measures of the Recent southwestern specimens are larger than those of the Madura Cave specimens, but there is overlap in many measures. A comparison of the Madura Cave material with specimens from Hasting's Cave, Western Australia (TMM 40236-3, -7, -8; PM 7272-81, PM 25510-15) shows that the remains from these two localities are alike both in size and morphology.

The smaller size of *Isoodon* from the drier areas of Australia has been noted in other studies. Wakefield (1964, pp. 494-498) reported that *Isoodon* from

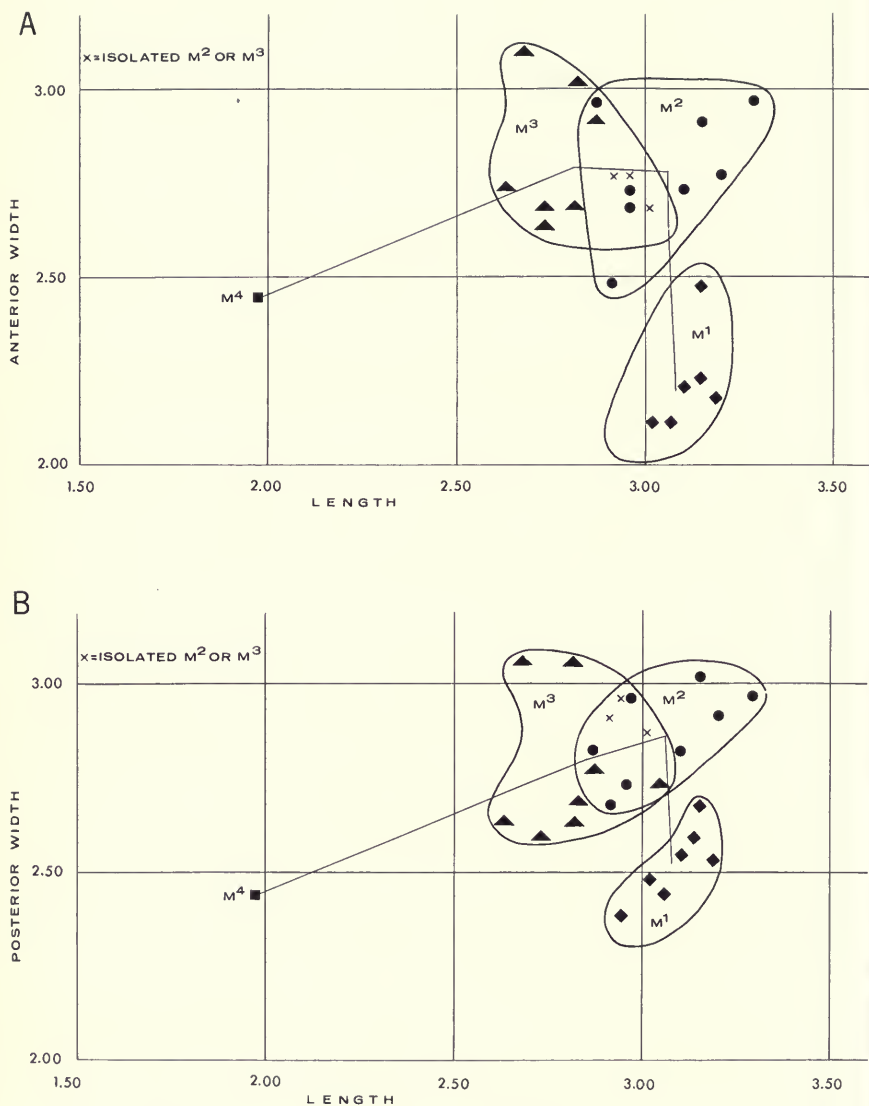
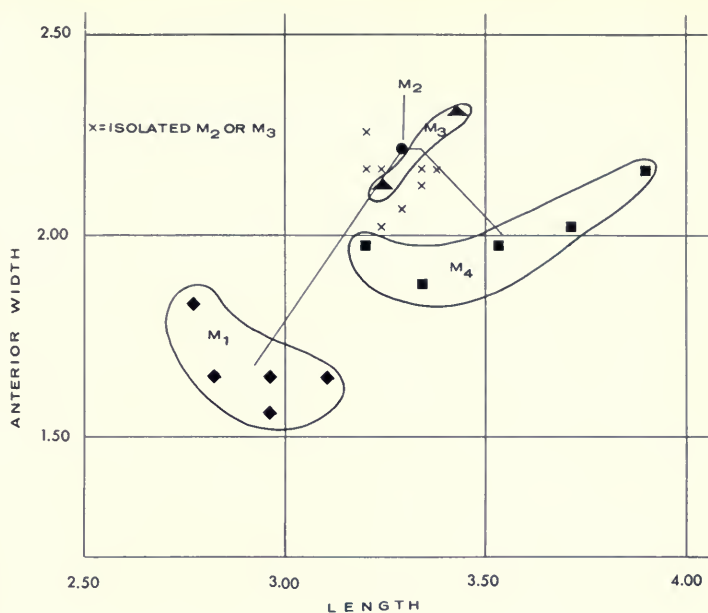


FIG. 13. *Isodon obesulus* from Madura Cave. In A & B, bivariate plots of molar tooth measures of length vs. anterior width and length vs. posterior width are shown. The solid symbols designate teeth whose positions are known with certainty; the x symbols indicate isolated M²s and M³s, which we cannot distinguish from one another with certainty.

C



D

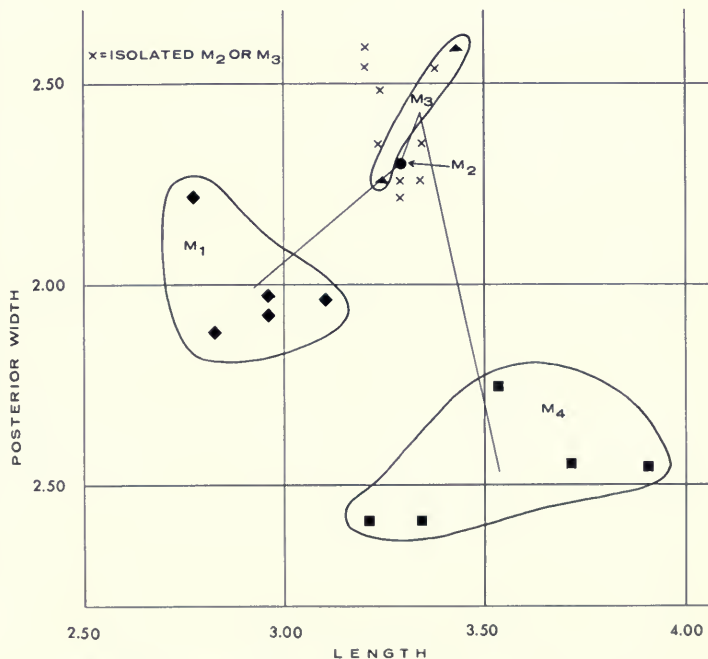


FIG. 13. In C & D, similar plots for the lower molars show extensive overlap of M_2 s and M_3 s. Isolated teeth indicated by x. Straight lines connect the midpoints of the plots for adjacent teeth.

TABLE 5. Numerical data on dentitions of various fossil and Recent samples of *Isoodon obesulus*.

Variate	Madura Cave			Recent, southern Western Australia			Fossil, southern Western Australia			Hasting's Cave, Western Australia			FM 98899 Tasmania
	N	Observed range	Mean	N	Observed range	Mean	N	Observed range	Mean	N	Observed range	Mean	
M ¹ L	4	3.01-3.15	3.08	3	2.96-3.29	3.09	2	3.24-3.29	3.27	1	—	3.06	3.34
AW	4	2.12-2.49	2.24	3	2.21-2.63	2.37	2	2.26-2.59	2.43	1	—	2.16	2.44
PW	4	2.44-2.68	2.54	3	2.49-2.87	2.63	2	2.54-2.77	2.66	1	—	2.59	2.77
M ² L	8	2.87-3.29	3.06	3	3.10-3.34	3.18	3	3.15-3.29	3.21	3	2.91-3.01	2.96	3.57
AW	8	2.49-2.96	2.78	3	2.59-3.20	2.89	3	2.68-3.20	2.93	3	2.54-3.06	2.76	3.01
PW	8	2.68-3.01	2.86	3	2.63-3.29	2.98	3	2.82-3.20	3.01	3	2.82-3.20	2.98	3.15
M ³ L	9	2.63-3.06	2.81	2	2.96-3.06	3.01	3	3.01-3.34	3.14	3	2.82-3.15	2.99	3.20
AW	9	2.63-3.10	2.79	2	3.20-3.57	3.39	3	3.06-3.29	3.20	3	3.06-3.29	3.17	3.20
PW	9	2.59-3.06	2.79	2	3.20-3.43	3.32	3	2.96-3.29	3.12	3	2.87-3.29	3.12	3.15
M ⁴ L	1	—	1.97	2	2.26-2.68	2.47	1	—	2.82	2	2.16-2.26	2.21	2.40
W	1	—	2.44	2	2.73-2.96	2.85	1	—	2.49	2	2.49-2.59	2.54	2.49
M ₁ L	5	2.77-3.01	2.92	2	3.01-3.29	3.15	1	—	3.24	2	2.87-2.91	2.89	3.06
AW	5	1.55-1.83	1.67	2	1.74-2.07	1.91	1	—	1.74	2	1.65	1.65	1.97
PW	5	1.88-2.21	1.99	2	2.16-2.63	2.40	1	—	2.21	2	1.93-1.97	1.95	2.21
M ₂ L	1	—	3.29	2	3.53-3.78	3.66	1	—	3.57	5	3.15-3.78	3.35	3.29
AW	1	—	2.21	2	2.21-2.44	2.33	1	—	2.26	5	1.93-2.26	2.10	2.49
PW	1	—	2.30	2	2.59-3.10	2.85	1	—	2.68	5	2.35-2.68	2.45	2.63
M _{2 or 3} L	9	3.20-3.38	3.28	—	—	—	—	—	—	—	—	—	—
AW	9	2.02-2.26	2.13	—	—	—	—	—	—	—	—	—	—
PW	9	2.21-2.59	2.40	—	—	—	—	—	—	—	—	—	—
M ₃ L	2	3.24-3.43	3.34	2	3.71-3.76	3.74	2	3.62-3.67	3.65	7	3.15-3.78	3.54	3.85
AW	2	2.12-2.30	2.21	2	2.35-2.49	2.42	2	2.30-2.54	2.42	7	2.12-2.44	2.26	2.49
PW	2	2.26-2.59	2.43	2	2.68-2.91	2.80	2	2.73-2.82	2.78	7	2.12-2.82	2.44	2.63
M ₄ L	5	3.20-3.90	3.54	2	3.85-4.18	4.02	1	—	4.14	5	3.57-4.09	3.78	3.95
AW	5	1.88-2.16	2.00	2	2.21-2.35	2.28	1	—	2.16	5	1.93-2.16	2.04	2.44
PW	5	1.41-1.74	1.53	2	1.97-2.12	2.05	1	—	1.79	5	1.50-1.65	1.56	1.97

Holocene deposits in the Fromm's Landing shelters are smaller than the modern ones from Western Victoria, but he gave no measurements. Small *Isoodon* from the arid zone of Australia were referred to *I. auratus* by Finlayson (1961). Marshall (1973) found no overlap in size in 13 dental measures of two samples of these small-sized *Isoodon* from central and Western Australia and a sample of *I. obesulus* from Victoria. His single specimen from a Holocene deposit at Lake Victoria falls within the range of the central Australian sample and accordingly was assigned to *I. auratus*.

The samples from Madura Cave and Hastings Cave are intermediate in size between those of *I. auratus* and *I. obesulus*, but are closer to the *I. obesulus* samples from southwestern Australia and Victoria (table 5). The significance of these size differences is not clear. Tate (1948) considered *I. auratus* to be a subspecies of *I. obesulus*. Marshall (1973) followed Finlayson (1961) and considered *I. auratus* to be a separate species. A revision of the genus is needed and is rendered more difficult in the face of the new evidence of the Madura and Hastings Caves samples. The Madura Cave material is referred to *I. obesulus* on the basis of the closer resemblance to modern samples of that taxon.

DISCUSSION

Isoodon obesulus is found today in southwestern and southeastern Australia, Nuyts Archipelago, Tasmania, and Cape York Peninsula. *Isoodon macrourus* is found along the east coast of Australia, Arnhem Land, and north Kimberley. *Isoodon auratus* is found in northwestern Australia, central Australia, and Barrow Island (Ride, 1970). The record of *I. obesulus* in the deposits of Madura Cave is close to halfway between its westernmost record in South Australia (Kangaroo Island) and its easternmost record in Western Australia. Its presence in units 1, 2, and 4-5 demonstrates that it was an element of the faunas of terminal Pleistocene and early Holocene times on the Nullarbor Plain and that its disappearance from the area is relatively recent. Its absence from unit 7 may be an accident of sampling because the total amount of material recovered from that unit is small. We have been unable to find a definite record of its occurrence on the Nullarbor Plain within historic times. It is found today in situations that are considerably more mesic than exist now on the Nullarbor Plain, but it is also found in ones with xeric conditions similar to those of the Nullarbor (and with similarly erratic rainfall).

Merrilees (1967) has pointed out that the broad distribution of *Isoodon* with respect to rainfall in Western Australia throws doubt on its use as an indicator of climatic change. Heinsohn (1966) in a study of *Perameles* and *Isoodon* in Tasmania found that *Isoodon* kept to brushy areas even when feeding, whereas *Perameles* fed in more open situations. This suggests that the disappearance of *Isoodon* from the Nullarbor Plain in the last 7,000 years was caused by the disappearance of the appropriate vegetation, not by increasing aridity as such, although the change in plant cover is almost certainly a result of increasing aridity.

Palynological studies at Madura Cave indicate a decrease in the mallee cover from about 5,000 to 6,000 years B.P. to present (Martin, 1973). This change is attributed to a combination of increased aboriginal fire pressure and a decrease in rainfall. The climatic interpretations based on the disappearance of *Isoodon* are consistent with the pollen record.

Chaeropus Ogilby, 1838*Chaeropus ecaudatus* Ogilby, 1838

MATERIAL

Trench 3, Unit 2

TMM 41106-695, right M² (fig. 16A)

Trench 3, Unit 3

TMM 41106-2763, edentulous right ramus fragment with alveoli of premolars (fig. 16D)

Trench 4, Unit 1, Level 1

TMM 41106-674, right M₂ or 3PM 27218, right M² or 3 (fig. 16B)PM 36828, right M₂ or 3 (fig. 16F)

Trench 4, Unit 2, Level 1

TMM 41106-670, right M₂ or 3TMM 41106-671, right M₂ or 3

Trench 4, Units 4-5

TMM 41106-683, right M₂ or 3 (fig. 16E)WAM 75.1.140, left M² (fig. 16C)

Trench 4, Unit 7, Level 2

WAM 75.1.141, right M₂ or 3TMM 41106-731, left M²TMM 41106-732, left M²PM 26333, left M₂ or 3

DESCRIPTIONS

This is the rarest bandicoot in the Madura Cave fauna, with only 13 specimens recognized as representing the taxon. The molar teeth are quite unmistakable because of their disproportionate labial and lingual hypsodonty. This condition gives the molars a characteristic diagonally sloping crown surface and renders them easily recognizable.

We have no Recent comparative material, hence comparisons are made with more complete sub-Recent fossils from other Nullarbor Caves, including: a right maxillary with M¹ from Weebubbie Cave (fig. 14A, PM 36806); a right maxillary fragment with M¹⁻³ (fig. 14C, TMM 41209-572) and a left maxillary fragment with M¹⁻⁴ (fig. 14B, TMM 41209-885), both from Webb's Cave; a right mandible with P₁, P₄, and M₃₋₄ from a cave between Kestrel #1 and #2 (fig. 15A-C, PM 36807); and a right mandible with P₁ and M₂₋₄ from Webb's Cave (fig. 15D-F, TMM 41209-573).

A characteristic of *Chaeropus* upper molar teeth is their shallow root condition. This makes them especially prone to dropping out after death. The alveoli of these teeth are distinctive too: the labial pair are deepest, but are very compressed anteroposteriorly, whereas the lingual two are fused into one, which is much expanded to accommodate the nearly completely fused roots supporting the paracone and hypocone (fig. 14A). A faint ridge marks the line of fusion and gives a slight constriction to the oval alveolar outline.

In the mandible, the alveoli of the molars are deeper to accommodate the

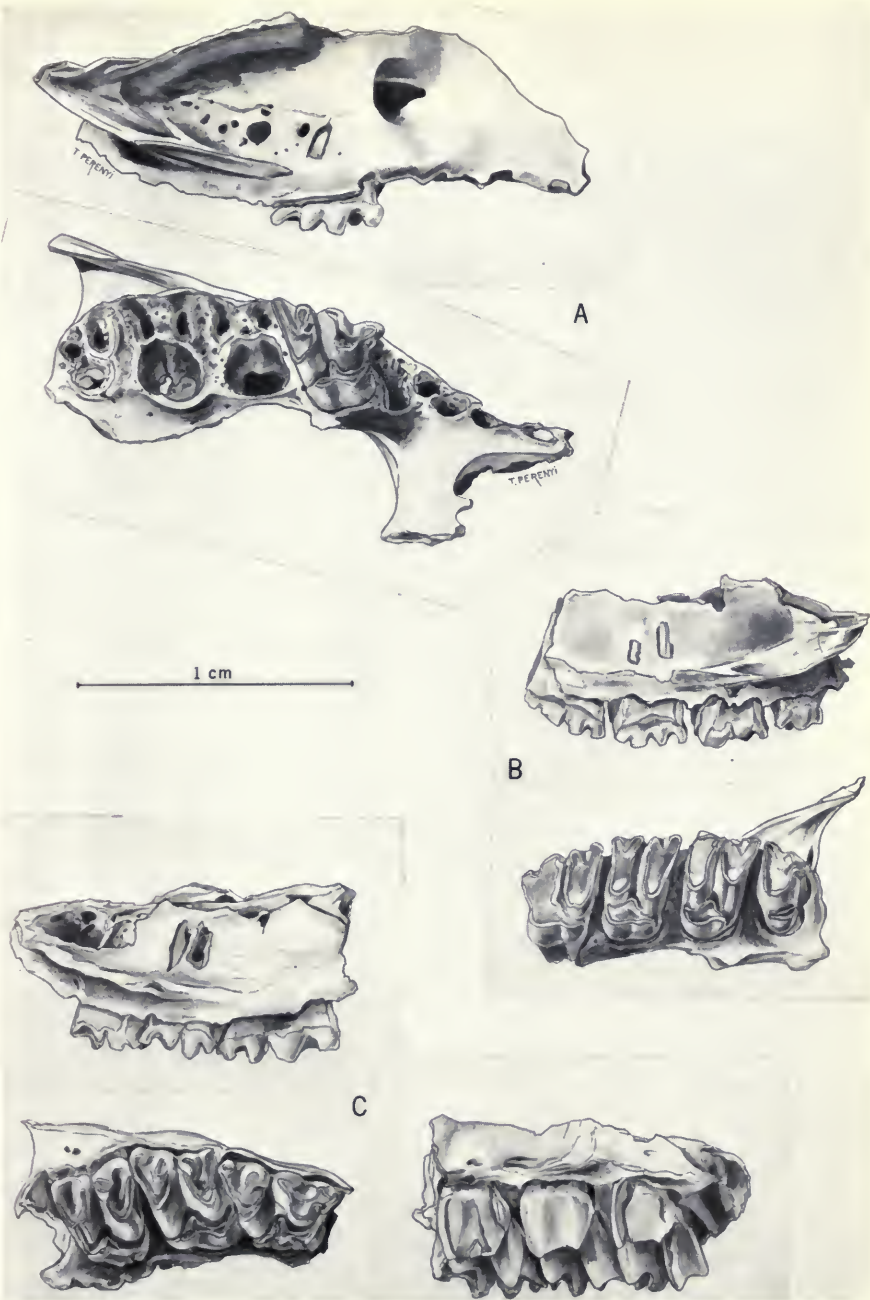


FIG. 14. *Chaeropus ecaudatus*, sub-Recent fossil specimens from several other Nullarbor Caves. A, PM 36806, a specimen from Weebubbie Cave (north of Eucla, Western Australia) that consists of a right maxillary with M^1 and that preserves the alveoli of the other molars, the premolars, and the canine. It is shown in labial and palatal views. B, TMM 41209-885, a left maxillary fragment with M^{1-4} from Webb's Cave, shown in labial and crown views. C, TMM 41209-572, a right maxillary fragment with M^{1-3} from Webb's Cave, shown in labial and crown views.



FIG. 15. *Chaeropus ecaudatus*, sub-Recent fossil specimens from several other Nullarbor Caves. A-C, PM 36807, a right mandible with P_1 , P_4 , M_{3-4} , and the alveoli of the rest of the teeth, from a cave between Kestrel #1 and #2, shown in lingual, occlusal, and labial views.

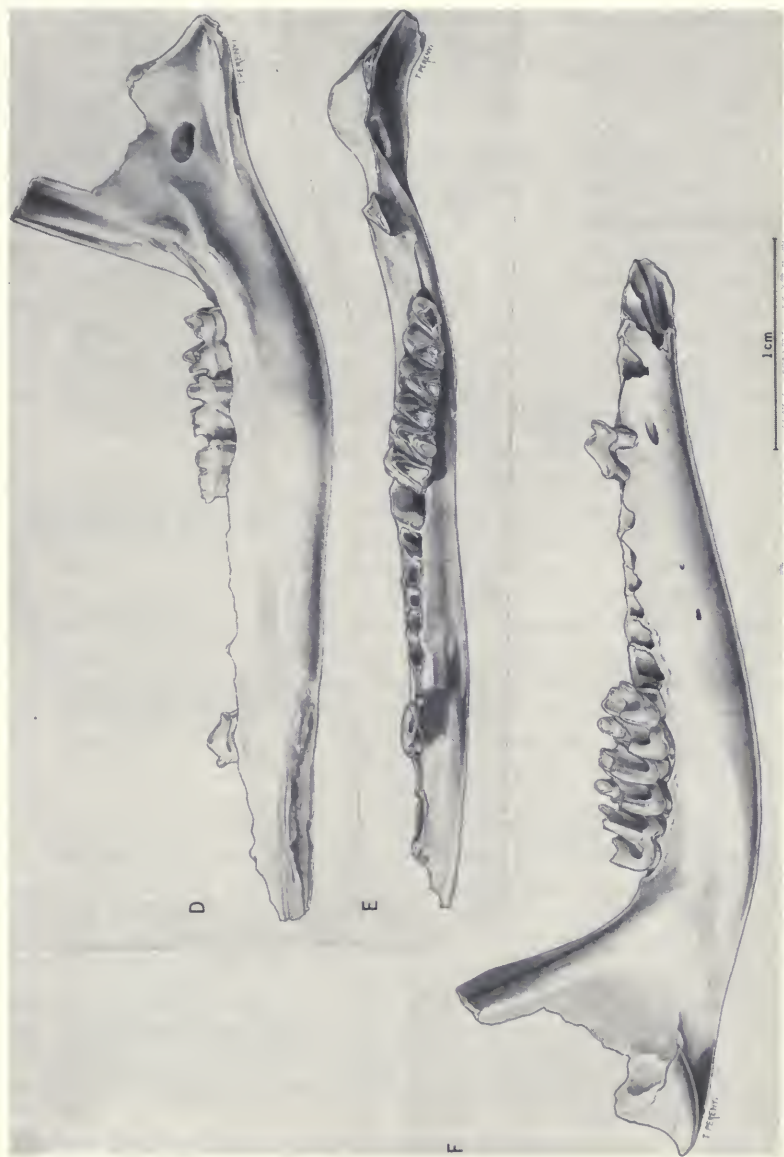


FIG. 15. D-F, TMM 41209-573, a right mandible with P_1 , M_{2-4} , and alveoli of the other teeth, from Webb's Cave, shown in lingual, occlusal, and labial views.

long, tapered roots of the molar teeth. The labial side of the alveolar margin is markedly lower than the lingual side (fig. 15C, F), and the ramus is deeper than in *Perameles*. The ascending ramus is wide from front to back, very different from its narrow condition in *Perameles*, and is much more like that in *Isoodon*.

Upper molars.—The upper molars are square in crown view and have a peculiar sort of tooth base hypsodonty, especially that part of the tooth underlying the protocone, hypocone, paracone, and metacone. The styler area of the tooth is significantly less hypsodont. No M^1 s or M^4 s are present in our Madura Cave sample.

The M^2 and M^3 are very similar (table 6; fig. 17A) but usually can be distinguished by features of the styler shelf. Two specimens from Webb's Cave (TMM 41209-572, -885; fig. 14B, C), which have M^{1-3} and M^{1-4} , respectively, show that M^2 has the metastyle more labially located than does M^3 . This results in reversed asymmetries in the shape of the ectoloph, especially in little-worn teeth. In M^3 , the metastyle protrudes farther labially than the other cusps; in M^2 , the parastyle is the more labial cusp. These specimens also show that the M^2 is further characterized by a rounded ridgelike extension of styler cusp 1 into the V formed by the ridges of the metacone. If these specimens are typical, it seems unlikely that any M^3 s are present in the Madura Cave collection. TMM 41106-695 (fig. 16A) is used to illustrate the upper molars.

The protocone is crescentic when unworn. It is higher and more extensive than the hypocone. Anteriorly, the protocone extends rootward onto the anterior face of the tooth. Posteriorly, it extends around the base of the paracone and into the central basin between the paracone and the metacone. The hypocone is a flattened column that expands toward its base. It is fused to the posterior limb of the protocone nearly to its apex. When worn, the posterior part of the protocone that projects labially into the curved valley appears to be a spur from the joined protocone and hypocone. Posteriorly, the hypocone extends rootward to the posterolingual corner of the tooth. There is a broad but prominent vertical groove on the lingual face of the tooth that separates the protocone and hypocone. This groove is better developed in *Chaeropus* than in *Isoodon*.

The paracone and metacone are very high, prominent cusps that, as in *Isoodon*, are the apices of V's that open on the labial border of the tooth. The metacone stands higher than the paracone. The paracone is joined to the parastyle (a) via the stylocone (j) by a straight eocrista (preparacrista or $I'x$). A straight postparacrista ($I'''a$) joins the paracone with the posterior side of the base of cusp k.

The metacone is joined to the metastyle by a postmetacrista (I'') and to the anterior side of the base of the mesostyle (cusp l) by a premetacrista (eocrista or $I'''b$). A distinct, small styler cusp m is present on TMM 41106-695 and PM 27218 (fig. 16A, B). It would be rapidly removed by wear and therefore is not distinguishable on worn teeth.

As in *Isoodon*, the cusp k and the mesostyle (cusp l) are about the same size and are larger than the parastyle and metastyle. Both cusps, k and l, are oval in cross section with their long axes oriented nearly transversely. Cusp k gives rise to a ridge that extends lingually from its apex for a short distance between the arms of the paracone crests, turns posteriorly, and joins the postparacrista. The mesostyle gives rise to a ridge that extends deeply into the V between the crests



FIG. 16. *Chaeropus ecaudatus* from Madura Cave. A, TMM 41106-695, a right M^2 shown in labial, crown, anterior (mesial), and lingual views. B, PM 27218, a right M^2 or M^3 shown in labial, crown, anterior (mesial), lingual, and posterior (distal) views. C, TMM 41106-684, a left M^2 shown in labial, crown, anterior (mesial), and lingual views. D, TMM 41106-2763, an edentulous right ramus fragment with the alveoli of the three premolars shown in dorsal and lateral (labial) views. E, F, TMM 41106-683 and -694, two right M_2 s or M_3 s shown in lingual, crown, anterior (mesial), and labial views.

TABLE 6. Numerical data on dentitions of two samples of *Chaeropus ecaudatus*.

Variate	Madura Cave			Other Nullarbor Caves (fossil)		
	N	Observed range	Mean	N	Observed range	Mean
M ¹ L	—	—	—	3	3.48-4.09	3.78
AW	—	—	—	3	2.49-2.68	2.59
PW	—	—	—	3	2.77-3.20	2.96
M ² L	4	2.96-3.01	2.97	2	2.68-2.87	2.78
AW	4	2.82-3.15	2.94	2	3.15-3.24	3.20
PW	4	2.77-3.01	2.89	2	3.06-3.24	3.15
M ³ L	—	—	—	2	2.68-2.87	2.78
AW	—	—	—	2	3.20-3.34	3.27
PW	—	—	—	2	2.91-3.06	2.99
M ⁴ L	—	—	—	1	—	1.88
W	—	—	—	1	—	2.54
M ₁ L	—	—	—	1	—	3.24
AW	—	—	—	1	—	1.41
PW	—	—	—	1	—	2.44
M ₂ L	—	—	—	2	3.15-3.20	3.18
AW	—	—	—	2	2.21-2.44	2.33
PW	—	—	—	2	2.30-2.59	2.45
M ₂ or ₃ L	6	3.24-3.52	3.35	—	—	—
AW	7	2.12-2.30	2.19	—	—	—
PW	7	2.16-2.35	2.27	—	—	—
M ₃ L	—	—	—	4	3.06-3.24	3.15
AW	—	—	—	4	2.12-2.30	2.24
PW	—	—	—	4	2.07-2.26	2.18
M ₄ L	—	—	—	5	3.38-3.57	3.44
AW	—	—	—	5	1.74-1.93	1.82
PW	—	—	—	5	1.27-1.41	1.37

of the metacone where it climbs partway up the labial face of the metacone. In some teeth (TMM 41106-732; WAM 75.1.140, fig. 16C), a short ridge extends from the lingual end of the mesostyle to the premetacrista. The labial ends of the V's are higher than the central areas, resulting in the formation of basins.

Mandible and lower molars.—The one mandibular fragment (TMM 41106-2763; fig. 16D) is slender and deep and has the alveoli of all the premolars. It is referred to *Chaeropus* on the basis of the distinctive form of the ramus and upon the presence of a prominent diastema in front of and behind the first premolar (compare fig. 16D with figs. 6D and 10E). Other peramelids have much less space between the first two premolars, P₁ and P₃, than does *Chaeropus* and the ramus is shallower.

No M₁s or M₄s were recovered, and M₂ and M₃ are so similar in size (table 6; fig. 17B) and form that we cannot be certain about a means of distinguishing them when they are found as isolated teeth. The lower molars of *Chaeropus* have the basic structure seen in most peramelids (figs. 15B, E; 16E, F). There is a high degree of the same sort of asymmetrical crown hypsodonty as in the upper teeth, particularly in the area underlying the protoconid and hypoconid. The trigonid is well defined in an unworn tooth, but its three cusps are close together, and the trigonid basin is small. The protoconid lies at the apex of an equilateral triangle formed by the anterior half of the eocristid and is joined to

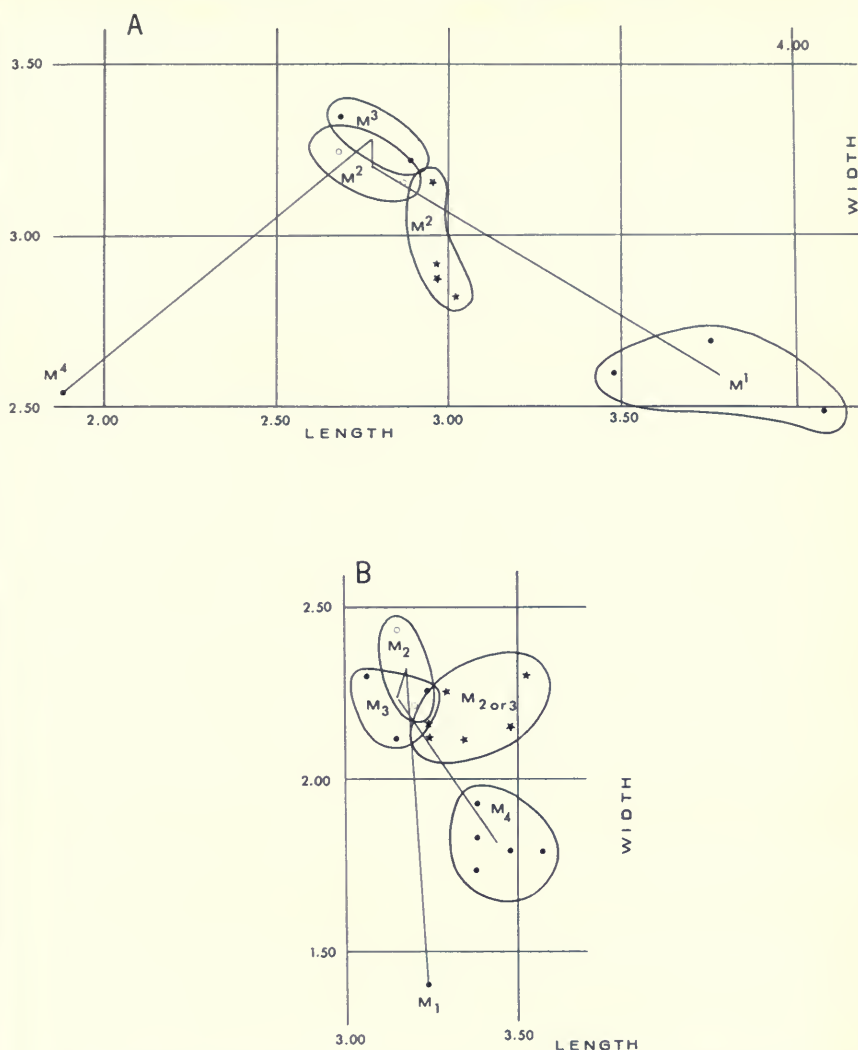


FIG. 17. Bivariate graphs showing plots of length vs. anterior width measures for each of the molar teeth of sub-Recent specimens of *Chaeropus ecaudatus* from several Nullarbor Caves. Stars designate those from the Madura Cave sample. Straight lines connect the midpoints of each tooth cluster of measures to provide the characteristic pattern for the species (compare with figs. 8C, D; 12A, B; 13A, C; 21A, B). Note extensive overlap of M²s and M³s and of M₂s and M₃s.

the paraconid and metaconid by the paralophid (paracristid, I') and metalophid (epicristid II', II''), respectively. Each of these ridges has an open V close to its midpoint, but there is no carnassial notch. There is no connection between the paraconid and metaconid, except where their bases abut one another.

The talonid is lower than the trigonid and is also V-shaped. The hypoconid lies at the apex of the V. A cristid obliqua (premetacristid I''b) joins it to the entocristid (V) at the anterior edge of the entoconid. The postmetacristid (I'')

joins the hypoconid to the small hypoconulid at the posterolingual corner of the tooth. The entoconid is circular in cross section and is located at the lingual edge of the tooth in the V formed by the posterior half of the eocristid. A weak crest (entocristid V) joins the anterior edge of the entoconid to the adjacent cristid obliqua.

Because the cristid obliqua does not join the protolophid, the hypoflexid extends all the way to the entocristid.

A cingulum is present at the base of the tooth between the protoconid and hypoconid. It may or may not bear a small cuspule. A large procingulum extends upward from the base of the protoconid to the base of the paraconid and incorporates a parastylid. It forms a prominent elongate cingular basin.

DISCUSSION

This species has been recorded as a living animal in two disjunct areas. One area includes southwestern New South Wales, much of South Australia, and the southern part of the Northern Territory. The other is a small area near Northam in the inland district of Western Australia. The Madura Cave specimens and notes by Merrilees (1968) and Archer (1972) demonstrate its former presence in an intermediate area. Its Recent occurrence in arid areas in South Australia suggests that it may have been widespread in the arid parts of southern Australia until very recently and that the disjunct nature of its known Recent distribution is the result of either a collecting bias or recent historic restrictions in its distribution. This is supported by the presence of its remains in surficial deposits in other caves of the Nullarbor Plain (Merrilees, 1968; Archer, 1972). Its presence throughout the sequence at Madura Cave indicates that it has had a long residence in this region and that it was one of the species able to tolerate the drying of the climate that took place at the end of the Pleistocene.

Macrotis Reid, 1837

Macrotis lagotis (Reid, 1837)

MATERIAL

Trench 3, Unit 1, Level 1

TMM 41106-32, edentulous right ramus fragment, juvenile

Trench 3, Unit 2

TMM 41106-73, left M₂ or 3

TMM 41106-56, right ramus fragment with M₂₋₃ and M₄ removed from crypt (fig. 20A)

TMM 41106-57, edentulous left ramus fragment of juvenile with alveoli of P₄-M₄

TMM 41106-58, edentulous right ramus fragment with alveoli of M₂₋₄

TMM 41106-59, edentulous right ramus fragment with alveoli of M₂₋₄?

PM 26336, left M¹ (fig. 19D)

PM 26337, right M₂ or 3

PM 26338, right M₂ or 3

PM 26339, right M₂ or 3

PM 26340, left M₁ (fig. 20B)

PM 26341, left M₂ or 3

PM 26342, edentulous left maxillary with alveoli of C-M¹ (fig. 19A)

PM 26343, left P₃ (fig. 20C)

Trench 3, Unit 2 (continued)

PM 26344, right P¹ or P³ (fig. 19B)PM 26345, broken left M² or ³PM 26346, right M₁PM 26347, broken right M² or ³PM 26348, left P₃ (or P₁)

Trench 3, Unit 2, Level 2

TMM 41106-53, left mandibular fragment with alveoli of two molars

TMM 41106-54, right M² or ³PM 26349, right M² or ³PM 26350, right M² or ³ (fig. 19E)PM 26351, left M¹PM 26352, right M² or ³PM 26353, left M² or ³PM 26354, left M₃ (or M₂)PM 26355, right M² or ³PM 26356, right M¹PM 26357, left P³ (or P¹)

Trench 4, Unit 1, Level 1

TMM 41106-476, right M² or ³TMM 41106-573, right M¹TMM 41106-575, left M¹ (fig. 19C)TMM 41106-584, left M₃ (or M₂)TMM 41106-611, left M¹TMM 41106-612, right M₃ (or M₂)TMM 41106-676, left M₁PM 26358, right M³ (or M²) (fig. 19G)PM 26359, right premolar, probably P₄PM 26360, anterior half of a left P³ or ¹PM 26361, right M³

Trench 4, Unit 2, Level 1

WAM 75.1.128, left P³?PM 26363, parastylar area of right M² or ³

PM 26364, lingual side upper molar

PM 26365, right M₃ (or M₂)PM 26366, right M² or ³PM 26367, right M² or ³PM 26368, left M² or ³PM 26369, left M⁴ (fig. 19H)PM 26370, left M₁PM 26921, right M² or ³PM 26922, right M² or ³PM 26923, left M² or ³

Trench 4, Unit 2, Level 2

PM 26924, left M¹PM 26925, right M² or ³PM 26926, right M₃PM 26927, left M¹

Trench 4, Unit 2, Level 2 (continued)

PM 26928, right M₂ or 3PM 26929, left M₁PM 26930, right M₁

Trench 4, Units 4-5

PM 26931, edentulous right ramus with alveoli of P₄-M₄ (fig. 20D)PM 26932, left M¹PM 26933, left M¹PM 26934, right M₂, 3, or 4PM 26935, left M₂ or 3

Trench 4, Units 4-5 (continued)

PM 26936, left M₃ (or M₂)PM 26937, right M¹PM 26938, left M² or 3PM 26939, right M¹PM 26940, left M₃ (or M₂)PM 26941, right M₄PM 26942, edentulous left ramus with alveoli of P₁-M₄ (fig. 20E)PM 26943, edentulous left ramus with alveoli of M₁-4PM 26944, left M₃ (or M₂)PM 26945, right M² or 3 (fig. 19F)PM 26946, anterior half, left M₂ or 3PM 26947, right M² or 3PM 26948, left M¹PM 26949, anterolabial corner of left M²PM 26950, trigonid of right M₂ or 3

PM 26951, left upper molar

PM 26952, trigonid of right lower molar

PM 26953, right M₁

PM 26954, trigon of right upper molar

PM 26955, right M³ (or M²)PM 26956, left M² or 3PM 26957, left M² or 3PM 26958, right upper molar fragment, probably M² or 3PM 26959, left P¹ or P³PM 26960, left premolar, probably a P₄PM 26961, right premolar, probably a P₄PM 30549, right M₁PM 30550, left M₁

Trench 4, Unit 7

PM 26963, left M² (or M³)

Trench 4, Unit 7, Level 1

PM 26964, left M² (or M³)PM 26965, left M³ (or M²)PM 26966, right M₁

PM 34417, edentulous ramus fragment

Trench 4, Unit 7, Level 2

WAM 75.1.129, edentulous right maxillary fragment with alveoli of P³⁻⁴PM 26967, right ramus with alveoli of P₄-M₃

Trench 4, Unit 7, Level 2 (continued)

- PM 26968, right M²
- PM 26969, right M₃ (or M₂)
- PM 26970, left M² (or M³)
- PM 26971, left M₃ (or M₂)
- PM 26972, right M¹
- PM 26973, right M¹
- PM 26974, left M₁
- PM 26975, right M₂ or 3
- PM 26976, right M₂

Trench 5, Unit 5

- PM 26335, right ramus fragment with alveoli of P₁-M₂ (fig. 20F)
- PM 26977, left M₂ (or M₃)
- PM 26978, left M₂ (or M₃)
- PM 26979, left M₃ (or M₂)
- PM 26980, right M³ (or M²)
- PM 26981, left M¹ fragment
- PM 26982, left M¹ fragment
- PM 26983, right M² or 3
- PM 26984, left M² or 3
- PM 26985, partial right M² or 3

Trench 5, Unit 5 or 6?

- PM 26986, left M₁
 - PM 26987, left P₃ (or P₁)
 - PM 26988, right P₃ (or P₁)
 - PM 26989, left P₃
- } possibly from the same individual

DESCRIPTIONS

Skull.—Very little cranial material of this species is represented in the Madura collection. Most of the specimens represent immature individuals, probably indicating that owls were the predators responsible for bringing the material to the cave. An adult *Macrotis* is probably too large to be regularly taken by owls.

One edentulous left maxilla of a juvenile (PM 26342, fig. 19A) is the only specimen that represents the skull. It has alveoli for the canine, the first two upper premolars, and dP⁴, and the M¹. The developing alveolus for the unerupted P⁴ is located lingual to that of the dP⁴. The infraorbital foramen is located above the anterior edge of the alveolus of M¹. It is elliptical in cross section and opens into a broad rounded groove on the lateral face of the maxilla.

A comparison of the Madura Cave specimen with the skull of a Recent specimen (FM 35331; fig. 18) reveals no differences that are not the result of the difference in ontogenetic age. The Madura Cave specimen is slightly younger, and the anterior part of the maxillary that carries the premolars is relatively shorter than in the Recent specimen.

Upper premolars.—Several upper premolars have been recognized. In one of them (PM 26344), a worn right P¹ or P³, the form agrees well with the modern comparative specimen. The tooth is double rooted, and the anterior root has a distinctive, markedly curved appearance. There is a single, large, central cusp with rounded crests. The anterior crest is very weak, and there is no anterior

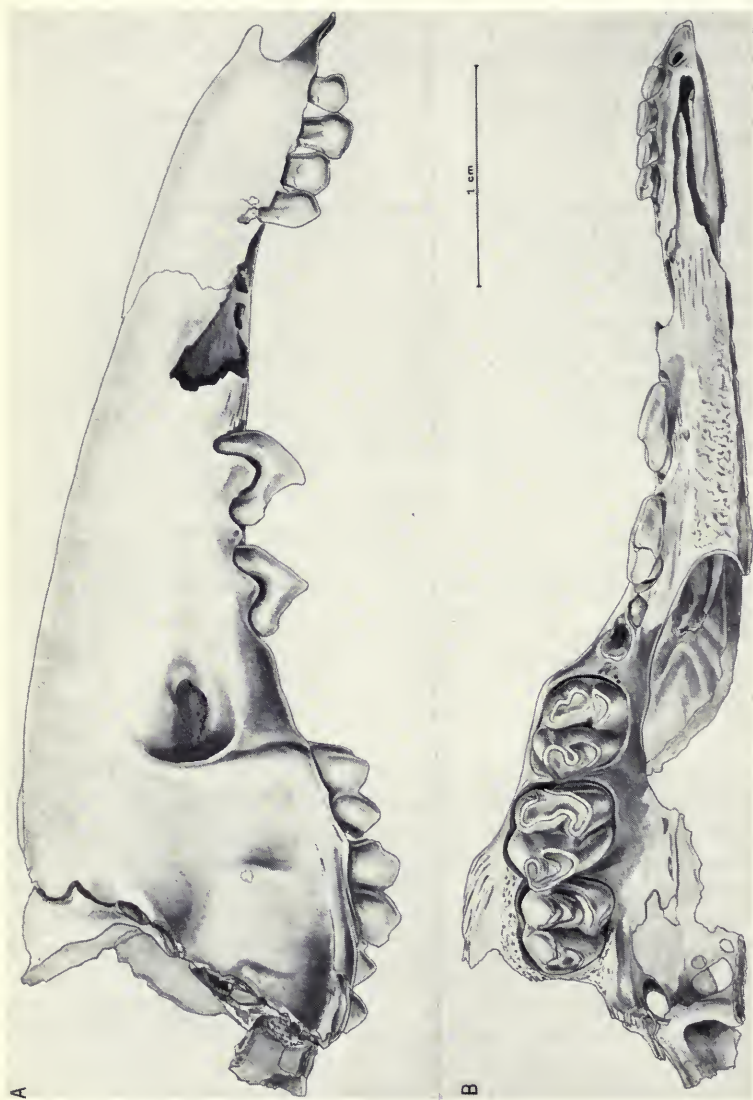


FIG. 18. *Macrotis lagotis* (Reid), a Recent juvenile specimen from Woyaline Wells, Pingelly, Western Australia. A & B, Right lateral and occlusal views of the facial-palatal portion of the skull. The I¹ and canine have been lost from their sockets, and the dP¹ had either been shed shortly before the animal was taken or it too has been lost from its socket. P⁴ and M³ are still within their crypts, the latter beginning to erupt.



FIG. 18. C & D, Left mandible shown in medial and occlusal views. The dP_4 is in place but is reversed front to back (probably an artifact of preparation), and the P_4 can be seen beneath (and in front of) it within its own crypt. The I_1 has been lost and has been drawn in by reversing that of the right side.

cingular cuspule. The posterior crest runs to a posterior cingular cuspule that shows wear lingually. The crown is slightly narrower than that of the modern specimen when viewed occlusally. Another specimen (WAM 75.1.128), a left P^3 (or P^1), is also worn. It is wider in the area of the posterior root than is PM 26344 and the recent specimen, and the anterior crest of the central cusp is more distinct as in the recent specimen. In PM 26959, a left P^1 or P^3 , there is a minute but distinct anterior cingular cuspule. None of the other teeth shows this feature, nor does the modern specimen. In PM 26357, a left P^3 or P^1 , the profile is unusual in that instead of being convexly curved from crown tip to root tip, here there is a slight concavity between the tip of the cusp and the base of the crown.

Upper molars.—The upper molars, with the exception of M^4 , are roughly rectangular in occlusal view when unworn. When worn, they become more square. The M^{1-3} have achieved this shape by an enlargement and lingual movement of the metacone rather than by the addition of a hypocone as in *Isoodon* and *Chaeropus*. The M^4 has the shape of a rounded triangle. All have massive rounded cusps and tooth base hypsodonty that is more developed on the lingual half of the tooth.

The M^1 is characterized by the presence of a well-developed parastyle with a medially directed crest that joins the paracone so as to delimit a tiny basin and the crowding together of the subequal-sized paracone and stylocone. The metacone is the largest cusp. It has the shape of an asymmetrical crescent in occlusal view, with the short anterior horn extending to the base of stylar cusp I. The longer posterior horn joins the metastyle. The protocone is the lowest major cusp on the tooth. It is elongated anteroposteriorly and reaches from the anterolingual corner of the tooth to the metacone. There is no connection with the parastyle.

Stylar cusp I is the tallest cusp on the tooth. It is rounded anteriorly where it is separated from the stylocone by a sharp valley. It is compressed posteriorly into a ridge that approaches but does not join the metastyle in the unworn state. With wear they become joined. A slight bulge on this ridge might represent stylar cusp m (PM 26336, PM 26351). Specimens TMM 41106-573 and 41106-575 (fig. 19C), although little worn, do not show this feature. Wear results in a joining of the metacone and stylar cusp I around the posterior part of the tooth and at a later stage in the joining of the paracone and stylocone, which in still later stages are joined to the protocone.

The M^2 and M^3 are so similar that they will be treated together. The stylocone and stylar cusp I are nearly equal in size and height and are the two highest cusps on the tooth. In the M^2 , the anterior face of stylar cusp I usually has a ridge (PM 26350 lacks this ridge: fig 19E), which is absent on the M^3 . The labial face of the stylocone of the M^2 bulges more than in M^3 , and the base of the enamel swings sharply toward the parastyle. In the M^3 , the labial surfaces of these two cusps bulge more nearly equally, and the labial enamel line does not turn toward the parastyle. The posterior face of the stylocone is ridged, usually better developed in the M^2 .

The metacone is the largest cusp. It is like that of the M^1 , with a long posterior part that extends around the posterior part of the tooth and joins the metastyle. The anterior arm swings labially to the base of stylar cusp I. In the M^3 , the crescents of metacone and paracone are not as disproportionate in size as in the M^2 , mostly because the crescent of the metacone is tighter in M^3 than it is in the M^2 .

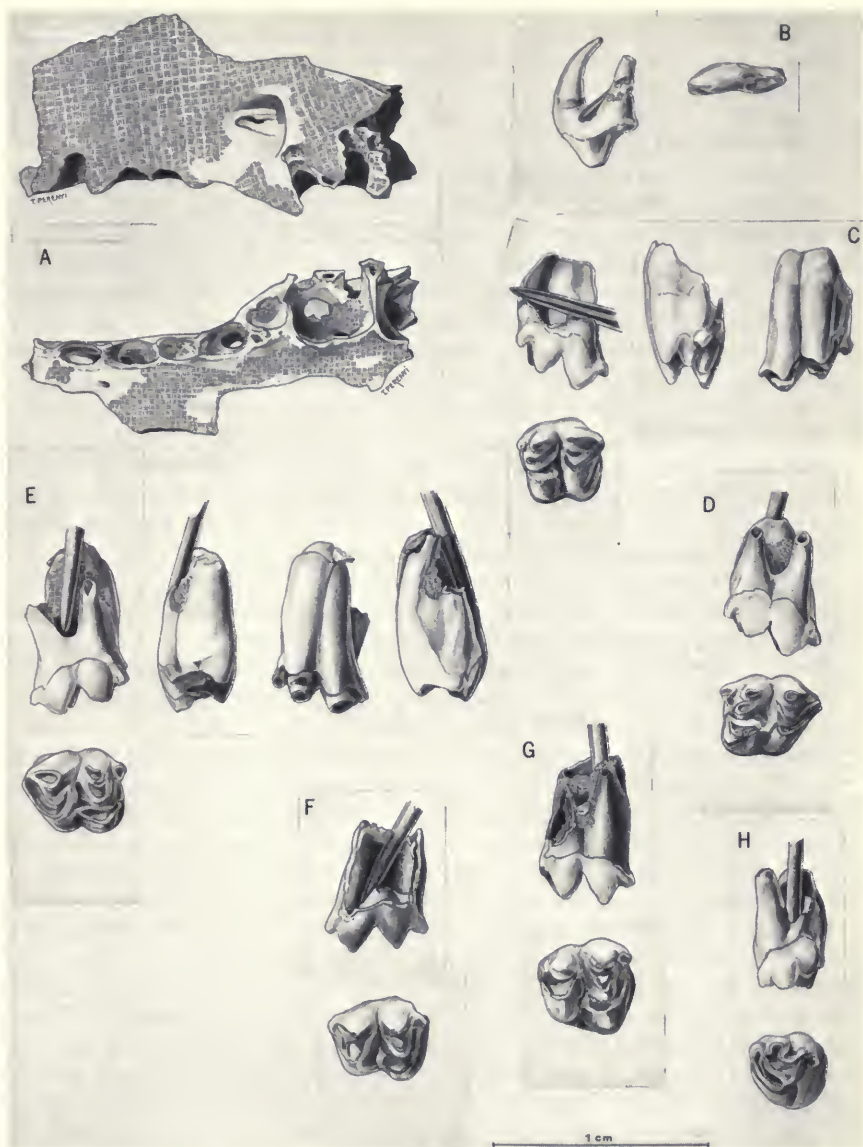


FIG. 19. *Macrotis lagotis* specimens from Madura Cave. A, PM 26342, an edentulous left maxillary fragment with the alveoli of C, P₁, P₃, dP₄, M₁₋₂, shown in labial and palatal views. Note the characteristic, large molar alveolus for the root of the protocone (and hypocone) which can be seen in the palatal view. Note too that the dP₄ had its two roots fused. B, PM 26344, a right P¹ or P³ shown in lingual and crown views. C, TMM 41106-575, a left M¹ shown in labial, mesial, lingual, and crown views. D, PM 26336, a left M¹ shown in labial and crown views. E, PM 26350, a right M² or M³ shown in labial, mesial, lingual, distal, and crown views. F, PM 26945, a right M² or M³ shown in labial and crown views. G, PM 26358, a right M³ or M² shown in labial and crown views. H, PM 26369, a left M⁴ shown in labial and crown views.

The protocone is the lowest major cusp. It extends from the base of the metacone around the anterolingual corner of the tooth and joins an anterior cingulum that continues to the parastyle. The paracone is V-shaped, with the anterior arm joining the base of the stylocone at the notch between the stylocone and parastyle.

In unworn or little-worn teeth, M^2 can be distinguished from M^3 by its narrower anterior absolute (but not relative) width (fig. 18B). This is demonstrated by the Recent specimens that have both teeth present in the maxillary. In the plot of the Madura Cave sample, we interpret the group with the narrower anterior width measure to be the M^2 s; that with the wider anterior width to be the M^3 s (fig. 21). At advanced wear stages in which all cusp, crest, and valley features of the crown have been worn away, the anterior width measures of M^2 and M^3 have become reversed. This reflects the nature of the crown hypsodonty in which the taper causes the anterior width vs. transverse proportions to shift at the different heights (wear stages).

The M^4 is a three-rooted tooth with the shape of a rounded triangle in cross section (fig. 19H). The posterior part of the tooth is reduced. The paracone is the largest cusp on the tooth. It is crescentic, with the anterior arm joining the base of a reduced stylocone. The posterior arm ends against a small cuspsule on the labial edge of the tooth. A well-developed anterior cingulum extends from the parastyle to the base of the paracone or a fused paracone-protocone. The latter alternative is suggested by the shape of the worn crescent. The posterior edge of the tooth is marked by a small cuspsule. Wear removes these features early in the life of the tooth. The result is an enamel ring surrounding the dentine core of the tooth.

Mandible.—Three specimens (fig. 20A, F, D), TMM 41106-156, PM 26335, and PM 26931, provide the basis for the description of the mandible of *M. lagotis* from Madura Cave. The horizontal ramus is characterized by its rapid increase in width at M_1 to accommodate the wide molars. The entire ramus is twisted so as to turn the anterior alveoli outward. A mental foramen is located under the P_1 . The posterior end of the symphysis is located between P_1 and P_2 .

The anterior edge of the ascending ramus makes a high angle (more than 45°) with the tooth row. The masseteric fossa is broad and bordered by ridges that become better defined with age. The ventral ridge of the masseteric fossa is enlarged above the angular process and forms a tubercle. A flattened rugose ridge extends from this tubercle onto the lateral edge of the angular process. The mandibular foramen, which is located in a broad, posteriorly open groove, opens near the anterior edge of the base of the angular process. The condyle is located closer to the top of the coronoid process than to the angular process. Its articular surface is almost circular. It is slightly concave transversely and convex anteroposteriorly.

Lower premolars.—Eight lower premolars have been recognized. Five of them (PM 26343, 26348, and PM 26987-9) are very much alike and are comparable to P_1 and P_3 of the modern form. They consistently differ from the modern form in having a wider posterior half of the crown base. They all show traces of two subsidiary cusps associated with the crests of the primary cusp, one on each crest. In the modern specimen, only one of the four teeth bears one of these features. On some of the fossils, there is a slight bulge where the anterior cingular cusp might be expected, but none has a cuspsule.

The P₄s (PM 26359 and PM 26960-1) are shorter anteroposteriorly than the other premolars, and the crown base is proportionately wider. The crown has a central cusp as its main feature, and this is laterally compressed and has anterior and posterior crests. The cingulae show variation. There is a weak anterior cingulum enveloping the anterior quarter of the crown base. On two (PM 26960-1), there is a small cusp present, and on one (PM 26359), this cusp is missing, and instead on the anterolingual side there are two minute cuspsules tight against the base of the central cusp just where the cingulum rises slightly before it merges into the base of the central cusp. All have a distinct posterior cingular cusp at the rear end of the posterior crest, usually somewhat lingually situated. In PM 26960 and 26961, short cingulae extend forward from this cusp, one on each side along the crown base margin for up to a fourth of the length of the tooth. In PM 26359, from the rear side of this posterior cingular cusp or heel, a weak cingulum runs down and labially across the midaxis of the tooth and then rises and runs forward for about one fourth the length of the tooth to merge with the base of the main cusp. It bears two minute, freestanding cuspsules. There is no lingual cingulum going off from this posterior cusp as in the other teeth.

Lower molars.—The M₁ of *M. lagotis* is elongate and tapers toward the anterior end. There is considerable tooth base hypsodonty beneath the protoconid as compared with the lingual side of the tooth where there is little or none and a much greater development of tooth base hypsodonty beneath the hypoconid similar to that of the labial side of the rest of the molars. The trigonid is narrow and small and variable in its development. It is slightly raised above the talonid, which is much wider. The protoconid and metaconid are subequal in size and height and are connected by a weakly developed epicristid (II' and II'') that runs across the valley between the cusps to connect to their back edges. The protoconid part of the epicristid lies just ahead of a better developed postparacristid (I'''a).

The paraconid is the smallest and lowest trigonid cusp, but it is better developed than on the Recent comparative specimen (FMNH 35331; fig. 18D). It lies ahead of the metaconid, appressed against its base. There usually is a connection to the protoconid by a paracristid (I'). In PM 26930, PM 26953, and PM 26966, this is a weak connection, but in PM 26370, PM 26974, and PM 30549, it is a stronger one, and in PM 26340 (fig. 20B), the ridges from each cusp are strong yet they fail to meet in the valley. In PM 26346, PM 26929, and PM 26986, there are not even any ridges suggestive of a connecting crest.

There is always a parastyloid that is low and lies anterior to the paraconid, near the crown base at the anterolingual corner of the tooth. It too varies in size and in the extent to which it tends to be extended labially into a short cingular ridge. In most, it is nearly a small cone, whereas in PM 26346, PM 26370, PM 26974, and PM 30549, there is an expressed tendency for the cingular crest to form.

In the talonid, the entoconid and hypoconid stand about equally high in an unworn tooth, but the latter, with its extreme crown base hypsodonty, is far larger. The entoconid is rounded posteriorly and ridged from its crest both anteriorly and anterolabially. The anterior crest runs toward the transverse central valley and bends labially without entering the bottom of the valley. The anterolabially directed crest also fails to reach the base of the cusp.

The hypoconid has a crescentic form with an anterior crest, the premetacristid

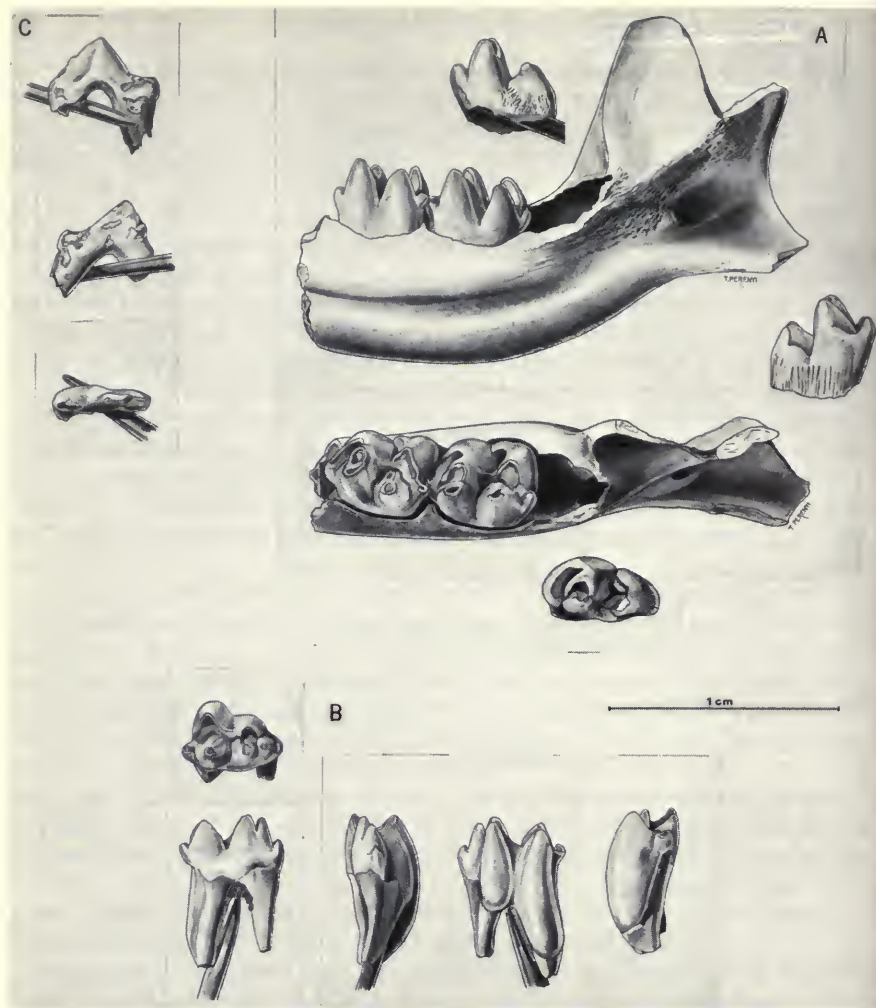
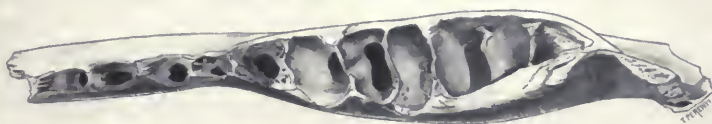
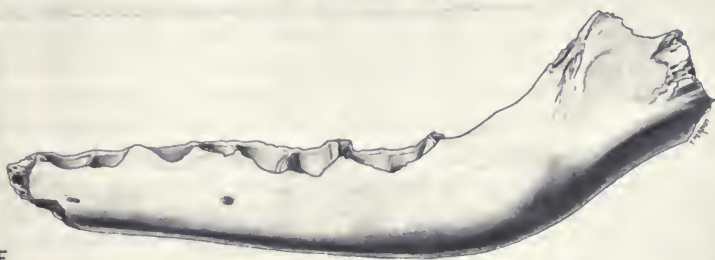
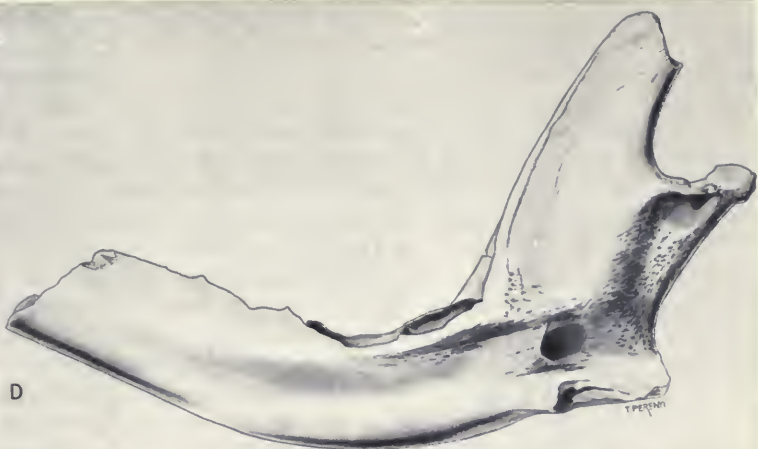


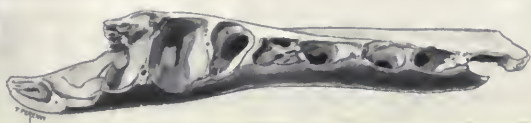
FIG. 20. *Macrotis lagotis* from Madura Cave. A, TMM 41106-156, a right mandibular fragment with half of the horizontal ramus, most of the coronoid and angular processes, but lacking the condyle. M_2 and M_3 are in place, and the unerupted M_4 has been removed from its crypt. The jaw is shown in medial and dorsal views, the M_4 in lingual, labial, and crown views. B, PM 26340, a left M_1 shown in crown, lingual, mesial, labial, and distal views. C, PM 26343, a left P_3 shown in labial, lingual, and crown views.

Opposite:

FIG. 20. D, PM 26931, an edentulous partial right mandible of a juvenile individual shown in lingual and dorsal views. Preserved is the ascending ramus and the posterior portion of the horizontal ramus, with part of the alveolus of dP_4 , part of the crypt of P_4 , the alveoli of M_{1-3} , and the crypt for P_4 . E, PM 26942, an edentulous left ramus with the alveoli of P_1 and P_3 , dP_4 , and P_4 at an early developmental stage within its crypt (the tip of the main cusp is broken off), the alveoli of M_{1-3} , and the crypt for M_4 . F, PM 26335, an edentulous right ramus fragment of a juvenile individual with alveoli of P_1 - M_2 including that for dP_4 and the crypt of P_4 , shown in labial and crown views.



1 cm



or cristid obliqua ($I'''b$), which runs anterolingually to join the postparacristid behind the protoconid above the transverse valley floor. The posterior crest of the hypoconid, the postmetacristid (I''), runs labially to join the hypoconulid at the posterolingual corner of the tooth. The hypoconulid is a rounded projection with a weakly developed crest connecting it to the base of the entoconid. In four specimens there is a spur from the postmetacristid to the base of the entoconid (PM 26340, PM 26370, PM 26986, and PM 30550). Occasionally there may be a small cingular cuspsule between the protoconid and hypoconid (PM 26370 and PM 26986), but usually there is no trace of this element.

Comparisons with the M_1 of two subfossil specimens (PM 4979 and PM 4980) from Murraelellavan Cave on the Nullarbor are very close. They have the crested parastyloid, but it is even more expanded and complex than in the Madura Cave specimens. Also, each has a spur from its postmetacristid to the base of the entoconid, and one (PM 4979) has the paracristid developed, the other does not, and neither has the small cingular cusplet between the protoconid and hypoconid as do a few of the Madura Cave specimens.

The major difference between the fossils and the Recent specimen is the much more reduced paraconid in the latter as well as a strong cingular cusp between protoconid and hypoconid.

The M_2 and M_3 are roundly rectangular teeth in crown view, and they are so similar that one description fits them both almost completely. The metaconid and entoconid are the highest cusps, and the former reaches slightly higher than the latter. The protoconid and hypoconid are smaller and lower, and in the unworn state the protoconid is slightly higher, but the hypoconid is a larger cusp with more open crescentic form than the protoconid—especially in M_2 . There is no paraconid on M_2 : the paracristid simply runs from the protoconid to the anterolabial base of the metaconid. In M_3 there is a small bulge at the union of crest and cusp that may be the homologue of the paraconid, and in one specimen, PM 26337, there is a weak crest from this "paracristid" to the parastyloid. The epicristid connects the back sides of protoconid and metaconid. The trigonid of M_2 is distinctly narrower than the talonid, whereas in M_3 both are about equal in width or the trigonid may be slightly wider. There is a heavy procumbent anterior cingulum that commences in a cuspsule one-half to two-thirds of the way up the anterolingual side of the protoconid. The cingulum runs forward and swings labially to form the stout parastyloid labial to the mid-axis of the tooth. It thereby cuts off a deep, curved depression between its crest and the anterolabial wall of the protoconid. There is a weak postparacristid that joins the cristid obliqua above the floor of the transverse valley. Usually the hypoconid in its hypsodonty suddenly flares forward, occluding the labial side of the transverse valley so that it abuts the back of the protoconid for the ventral one-half to two-thirds of the height of the crown beneath these cusps. An exception to this is seen on PM 26337 where the flare is gentle and the protoconid also flares backward a bit. In another specimen (PM 26365), neither cusp flares, they just gradually expand. The posterior arm of the hypoconid crescent, leading to the hypoconulid, sends off a spur to the base of the entoconid. The hypoconulid of M_2 is slightly larger than that of M_3 , and either tooth may have minute cingular cuspsules associated with it. In one specimen (PM 26337), an M_3 , there is no hypoconulid, and the postmetacristid just fades away without reaching the posterolingual corner of the tooth.

The M_2 s and M_3 s are similar in size and morphology but can be separated on

bivariate scatter diagrams of tooth length vs. anterior and posterior widths. In each case, M₂s are shorter than M₃s (fig. 21B). The scatter diagram of L vs. AW shows the M₂s to be narrower, too, so that there is a clear separation into two discrete groups. In M₃, the two width measures do not show a significant difference, and although there is a complete separation along the length scale, there is no gap between the clouds of points. Larger samples might be expected to show some overlap.

The M₄ has a well-developed trigonid and a reduced and posteriorly tapered talonid (fig. 20A). The protoconid and metaconid lie close to one another, about as in the M₁, and they are nearly equal in size. Both are somewhat crescentic. The posterior arm of each crescent descends, and they meet in the center along the back edge of the trigonid. The anterior arm of the metaconid is enveloped by that of the protoconid. This results from the more open crescentic form of the protoconid. The anterior cingulum is pronounced and is similar to those of M₂ and M₃. The two basins in the trigonid region, a central trigonid basin and an anterior cingular basin, are joined. The central basin that lies between the facing crescents of protoconid and metaconid is small and has an anterolingually directed valley leading from it. The anterior cingular basin lies transverse to the tooth axis, and at its lingual end it joins the lingual end of the valley of the central basin. There may or may not be a common exit to the lingual side of the tooth. A parastylid cusp is incorporated into the lingual terminus of the cingulum. The trigonid is raised above the talonid. The entoconid is the largest talonid cusp, and it is weakly crescentic. The hypoconid is very low and not well defined, and there is only the faintest trace of a hypoconulid. The talonid basin is triangular and deeply clefted labially.

Comparisons.—The M₁s from Madura Cave and those of young individuals from Murraelellevan Cave (PM 4872) have a well-developed parastyle. The more complete specimens in the Murraelellevan sample show that this feature is soon reduced, then eliminated by wear. One Recent specimen from Woyaline Wells (FMNH 35331; fig. 18A, B) has no parastyle on its M¹. Its absence cannot be attributed to wear because this specimen is a juvenile with M³ still incompletely erupted, with P⁴ and M⁴ within their respective crypts.

On M¹, the Madura Cave specimens have no anterior cingulum connecting protocone to parastyle as is seen in unworn specimens from Murraelellevan Cave. Such a cingulum is present on all the other molars of the Madura Cave materials and in unworn or little worn M²-M⁴ of all of our comparative specimens.

On M² of the Murraelellevan Cave specimen, the anterior ridge of the paracone also goes to the parastyle; in the Madura Cave specimens of M² and in M² of the comparative materials and in all M³s, this ridge goes toward the notch between the parastyle and stylar cusp 1.

Last molars are rare in spite of a relatively large number of specimens of *Macrotis* in the Madura Cave fauna. This correlates with the young age stages of most of the other teeth. The M⁴s and M₄s had not fully formed at the time of death. The other lower molars compare well in their main features to the available Recent and fossil materials.

DISCUSSION

Macrotis lagotis is known as a living animal from widely scattered areas in the dryer parts of Australia, including two localities, Ooldea and Rawlinna, on the

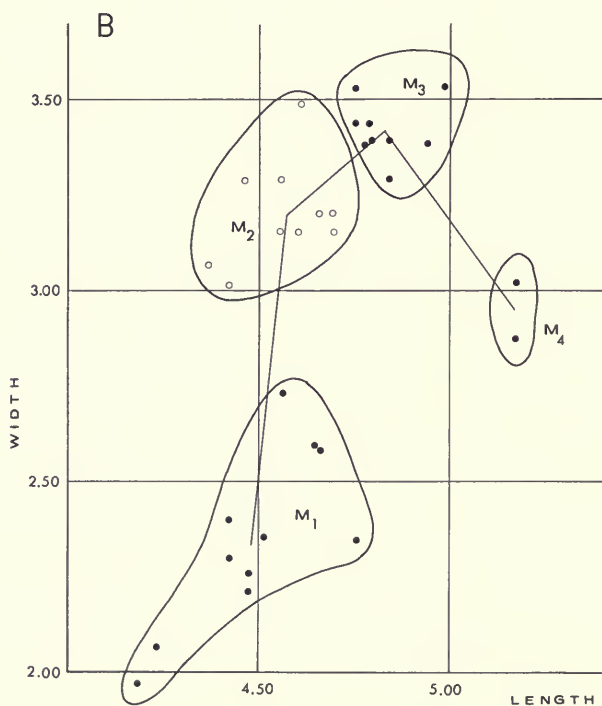
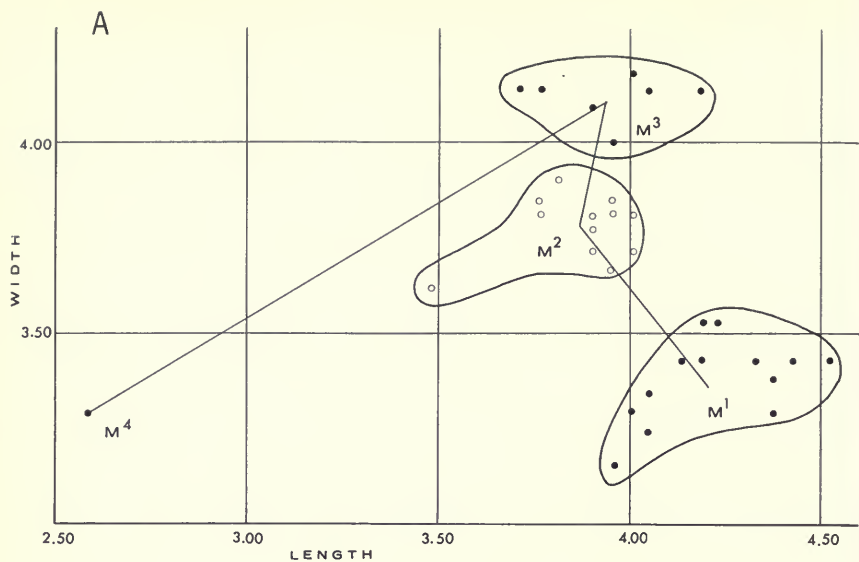


FIG. 21. Bivariate graphs of length vs. anterior width for the upper (A) and lower (B) molars of *Macrotis lagotis* from Madura Cave, showing complete separation of all molars. The means for adjacent teeth are connected by straight lines to form the patterns for the species. Measurements are in millimeters.

TABLE 7. Numerical data on upper dentitions of fossil and Recent samples of *Macroptis lagotis*.

Variate	Madura Cave				Other Nullabor Caves			Recent		
	Sample size	Observed range	Mean \pm standard error	Standard deviation	Coefficient of variation (%)	Sample size	Observed range	Mean \pm standard error	Sample size	Observed range
P ¹ L									6	3.76-4.42
W									5	1.03-1.55
P ³ L									6	3.90-4.32
W									5	1.32-1.65
P ⁴ L									4	3.15-3.90
W									4	1.55-1.97
M ¹ L	15	3.95-4.51	4.20 \pm .046	0.177	4.21				6	3.62-4.18
AW	14	3.15-3.53	3.36 \pm .033	0.123	3.64				6	2.96-4.56
PW	14	3.10-3.67	3.38 \pm .040	0.151	4.47				6	3.10-4.70
M ² L	12	3.48-4.00	3.86 \pm .042	0.146	3.78	3	3.95-4.14	4.04	6	3.48-4.23
AW	12	3.62-3.90	3.78 \pm .024	0.083	2.19	3	3.95-4.23	4.06	6	3.90-4.56
PW	12	3.20-3.90	3.55 \pm .054	0.188	5.30	3	3.62-4.00	3.78	6	3.53-4.56
M ³ L	7	3.71-4.18	3.93	—	—	4	3.62-4.09	3.82	6	3.53-4.14
AW	7	4.00-4.14	4.10	—	—	1	—	4.62	6	4.04-4.61
PW	7	3.53-4.00	3.64	—	—	1	—	4.00	6	3.38-4.42
M ⁴ L	1	—	2.59	—	—				4	2.59-3.67
W	1	—	3.29	—	—				4	2.91-4.23
										Mean

TABLE 8. Numerical data on lower dentitions of fossil and Recent samples of *Macrotis lagotis*.

Variate	Madura Cave				Other Nullarbor Caves				Recent				
	Sam- ple size	Observed range	Mean \pm standard error	Coefficient of variation (%)	Sam- ple size	Observed range	Mean \pm standard error	Standard deviation	Coefficient of variation (%)	Sam- ple size	Observed range	Mean	
P ₁ L	—	—	—	—	—	—	—	—	—	5	3.95-4.56	4.23	
W	—	—	—	—	—	—	—	—	—	5	0.94-1.18	1.06	
P ₃ L	—	—	—	—	—	—	—	—	—	6	4.32-4.98	4.58	
W	—	—	—	—	—	—	—	—	—	5	1.08-1.41	1.21	
dP ₄ L	—	—	—	—	—	—	—	—	—	2	2.12-2.30	2.21	
W	—	—	—	—	—	—	—	—	—	2	0.94-1.18	1.06	
P ₄ L	—	—	—	—	—	—	—	—	—	3	3.76-4.14	3.89	
W	—	—	—	—	—	—	—	—	—	3	1.55-1.74	1.65	
M ₁ L	11	4.18-4.75	4.48 \pm .052	0.173	3.84	3	4.75-4.84	4.78	—	6	3.76-4.84	4.39	
AW	11	1.97-2.73	2.35 \pm .068	0.227	9.66	3	2.35-3.40	2.70	—	6	2.16-3.06	2.59	
PW	11	2.73-3.29	3.01 \pm .049	0.161	5.35	3	2.87-3.06	2.96	—	6	2.96-3.90	3.49	
M ₂ L	10	4.37-4.70	4.57 \pm .036	0.113	2.48	9	4.28-4.89	4.60 \pm .063	0.190	4.12	6	3.95-5.03	4.42
AW	10	3.01-3.48	3.20 \pm .042	0.132	4.13	9	3.01-3.38	3.17 \pm .043	0.130	4.11	6	3.06-4.09	3.71
PW	10	3.38-3.85	3.62 \pm .048	0.152	4.19	9	3.20-3.85	3.53 \pm .062	0.186	5.28	6	3.34-4.65	4.14
M ₃ L	9	4.75-4.98	4.83 \pm .027	0.081	1.67	10	4.32-4.89	4.72 \pm .063	0.199	4.20	6	4.00-4.98	4.44
AW	9	3.29-3.53	3.41 \pm .026	0.077	2.25	10	3.06-3.67	3.37 \pm .062	0.196	5.80	6	3.24-4.51	3.92
PW	9	3.43-4.00	3.69 \pm .071	0.213	5.76	10	3.06-3.67	3.40 \pm .060	0.190	5.58	6	3.57-4.70	4.10
M ₄ L	1	—	5.17	—	—	2	4.42-4.47	4.45	—	—	4	4.09-5.47	4.66
AW	2	2.87-3.01	2.94	—	—	1	—	2.73	—	—	4	2.96-4.09	3.51
PW	1	—	2.30	—	—	1	—	1.88	—	—	4	2.16-3.43	2.85

Nullarbor Plain. These are the type localities of two of the six named subspecies of *Macrotis lagotis*, *M. l. nigripes* and *M. l. interjecta*. There is substantial geographic variation in size, but there are few other characters that have been the basis for the erection of a number of subspecies. The existence of extensive size variation between local populations cited by Mack (1961) is supported by a comparison of the range of size of various dental characters of the Madura Cave sample, the other fossil samples, and the Recent samples (tables 7 and 8). The Recent sample, which is geographically heterogeneous, shows the greatest range of size, the younger fossil material from other Nullarbor caves shows less, and the Madura Cave sample, the least. The small range of size of the Madura Cave sample (fig. 21) suggests that there was little change in size in the *M. lagotis* population in the Madura area over approximately 30,000 years (38,000 to 7,500 years B.P.).

It is not possible on the basis of the material available to us to show that the Madura Cave sample is closer to one of the above-mentioned samples than to any of the others. The species now seems to be divided into a number of local populations that show various minor morphological differences. *Macrotis lagotis* is another species that has been resident on the Nullarbor Plain for a long time and that was able to tolerate the changing conditions at the end of the Pleistocene. Brooker (1977) suggested two possible reasons for the absence of this species (as well as many others) since the 1930's and 1940's—the length and severity of the droughts of 1933 and 1935 and the repeated man-set fires, such as the bush fires of 1942.

SUMMARY

The four taxa of peramelids represented in the Madura Cave deposits, *Perameles bougainvillei*, *Isoodon obesulus*, *Chaeropus ecaudatus*, and *Macrotis lagotis* are described. All except *I. obesulus* are elements of the present (or historic) fauna of the Nullarbor Plain. *Isoodon obesulus* today lives in areas that are mostly more mesic than the Nullarbor Plain, but it is known from comparably xeric areas as well. Its presence in the Pleistocene and early Holocene deposits may indicate a change to drier conditions in this region since approximately 7,000 years B.P. Aside from a decrease in size in *Perameles bougainvillei* between units 4-5 (22,200 years B.P.) and unit 1 (7,500 years B.P.), no morphological trends were seen in any of these taxa over the time represented by the deposits sampled.

In the earlier sections, it was shown that units 2-5 of trench 3 and units 2-7 of trench 4 contained remains of a number of extant taxa that are no longer found living on the Nullarbor Plain. They are: *Antechinus flavipes*, *Phascogale calura*, *Parantechinus apicalis*, *Dasyuroides byrnei*, *Sarcophilus harrisii*, and *Thylacinus cynocephalus*. The first three taxa presently live in areas of southwestern and/or southeastern Australia that have more mesic climates than that of the Nullarbor Plain today. *Sarcophilus harrisii* and *Thylacinus cynocephalus* are only recently extinct on the Australian mainland, and their disappearance may have been more the result of the introduction of the dingo than of general environmental change (Archer, 1974; Calaby & White, 1967).

Dasyuroides byrnei is now found in a limited area of desert grassland and desert steppe in northeastern South Australia, southeastern Northern Territory,

and southwestern Queensland (Marlow, 1962). The disappearance of this species that lives today in an arid region seems anomalous. Clearly, the increased aridity had a secondary effect that adversely affected this animal.

The stratigraphic distribution of peramelids in the Madura Cave sequence is consistent with the interpretation of a change toward more arid conditions at the end of the Pleistocene.

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